Tinder for orang-utans:

comparing sexually selective cognition among Bornean orang-utans (*Pongo pygmaeus*) and humans (*Homo sapiens*)

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Tom Roth
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Table of contents

Preface

This dissertation is the result of a close collaboration between Leiden University, Apenheul Primate Park, and the European Endagered Species Programme (EEP) for orang-utans. In 2017, Thomas Bionda, Warner Jens (both Apenheul), and Mariska Kret (Leiden University) decided to team up with the goal of refining the orang-utan breeding programme by taking individual mate preferences into account. One promising approach to do this, was application of computerized tasks within the orang-utan breeding programme to identify such mate preferences in zoo-housed orang-utans. Until then, computerized tasks had mainly been used to study fundamental scientific questions. For instance, the bonobos (*Pan paniscus*) in Apenheul had been participating in multiple non-invasive experiments to study emotion perception (Kret et al., 2016; van Berlo et al., 2023). This research programme inspired the idea of finding a more practical application for such methods, in addition to fundamental questions.

One particular species for which such a practical application was considered useful was the orang-utan (*Pongo* spp.). Zoo-housed orang-utans have relatively low breeding success compared to other great ape species (Kaumanns et al., 2004), and their birth rate may have been too low to maintain a stable population size (Bemment, 2018). One potential reason for this is the solitary nature of orang-utans: they live a semi-solitary lifestyle (Roth et al., 2020), and group life may actually be a stressor for them (Amrein et al., 2014; Weingrill et al., 2011). At the same time, orang-utan females are known to be selective in their mate choice (Knott et al., 2009). This led to the idea of developing tasks that can assess orang-utan mate preferences, ultimately providing them with more control over their social environment, which could also lead to increased reproductive success. With this goal in mind, I started my PhD project in 2019, eventually resulting in this dissertation.

Currently, most captive breeding programmes do not take mate preferences into account, although a large body of literature shows that animals have higher reproductive success when allowed to choose their own mate (reviewed in Martin-Wintle et al., 2019). Instead, breeding recommendations are heavily based on genetic data and practical factors such as housing space. Admittedly, it has not been easy to incorporate mate preferences into breeding programmes: studies that find beneficial effects of incorporating mate choice often rely on behavioural measures during inter-individual interactions to identify mate preferences. Such methods are not feasible in zoo populations, where individuals are spread across multiple locations. This has led some authors to argue for long-distance methods, that allow identification of mate preferences even when individuals are housed in different facilities (Asa et al., 2011). In line with this idea, the current dissertation explores whether simple cognitive tasks are suitable for identifying mate preferences of zoo-housed Bornean orang-utans (*P. pygmaeus*). As it is challenging to validate such methods in orang-utans (e.g., by linking them to reproductive success), similar cognitive tasks were presented to a human sample in combination with measures of explicit mate preferences. Although results from humans are not directly generalisable, this approach may help identifying tasks that have the *potential* to determine mate preferences in zoo-housed orang-utans.

Given that practical research with animals rarely receives funding via conventional funders, it has been challenging to obtain sufficient resources to realise the project. In the end, this project is made possible by generous donations from multiple zoos within the orang-utan EEP: Allwetter Zoo, Apenheul Primate Park, Dublin Zoo, Ouwehands Dierenpark, Taipei Zoo, Zoo Barcelona, Zoo Osnabrück, Zoologischer Stadtgarten Karlsruhe, Zoo Zürich, & Wilhelma Zoologisch-Botanischer Garten. Furthermore, it is important to note that this research project was heavily impacted by the COVID19 pandemic. Especially during the start, when the risk of COVID19 for great apes was still unclear, no risk was taken and experiments were halted. Not surprisingly, this has had a large impact on the amount of data that could be gathered with the orang-utans. Therefore, the results presented in this dissertation mostly focus on attentional tasks. However, we are still broadening our scope by running new studies on this topic and hope that this will allow us to develop multiple suitable tasks encompassing different aspects of mate choice in the future, resulting in a more refined breeding programme.

Chapter 1

General introduction

Choosing a partner is one of the most critical decisions that humans make during their life. Even though it is important, the mechanisms underlying mate choice remain a mystery, because mate choice is such a complex and multifaceted phenomenon. Nevertheless, it has been established that cognition plays a pivotal role in finding a suitable mate. A broad definition of cognition encompasses perception, learning, memory, and decision making, and refers to all mechanisms that allow an individual to acquire, process, store, and act on external information (Shettleworth, 2010). This definition encompasses both fast, reflexive, subconscious processes, also referred to as implicit cognition, and slower, more versatile processes, also referred to as explicit cognition (Frith & Frith, 2008). In the case of mate choice, reflexive attention towards an attractive face could for instance be considered implicit cognition, while selecting the most attractive face out of a set would be considered explicit cognition.

The importance of cognitive processes in mate choice can clearly be observed in humans: when asking people to describe how they feel about their loved one or the first encounter with their loved one, they often refer to specific cognitive processes, such as attention, memory, and implicit associations. “I could not get my eyes off him”, “She immediately caught my attention”, or “I cannot get him out of my head”: almost everybody has used or heard such statements about a romantic partner. These cognitive processes in the context of mate choice have been termed *sexually selective cognition* (Maner & Ackerman, 2015; Box 1), which implies that exploring the cognitive mechanisms involved in mate choice and attractiveness can provide valuable insights into a complex phenomenon like mate choice.

Even though humans find it very easy to speak about mate choice in cognitive terms, we seem relatively reluctant to apply similar terminology to non-human mate choice. This is also reflected in research: while a plethora of studies has investigated the interplay between cognition and mate choice in humans, only few studies have started to explore this topic in our closest animal relatives. However, from an evolutionary perspective one would expect non-human animals to have analogous or homologous cognitive mechanisms that could help navigating the mate choice process (Bateson & Healy, 2005; Billington et al., 2020; Grammer et al., 2003). Interestingly, the impressive technological developments (e.g., touchscreens and eye-trackers) of the last two decades now allow us to study non-human cognition in more depth, and these developments have enabled researchers to investigate topics like emotion perception (e.g., Kret et al., 2016, 2018; Pritsch et al., 2017; van Berlo et al., 2023), theory of mind (e.g., Krupenye et al., 2016), and ingroup-outgroup bias (e.g., Kret et al., 2014; Lewis et al., 2021; van Berlo et al., 2023) in primates. Up until now, however, very few studies have applied these technologies to study cognition and mate choice in non-human animals, and especially great apes.

Box 1: sexually selective cognition

Sexually selective cognition (Maner & Ackerman, 2015) can be considered as an integration of evolutionary psychology, cognitive psychology, and motivation science. More specifically, the approach is concerned with how mating motivations influence cognitive processes in an evolutionarily adaptive manner. Sexually selective cognition aligns with evolutionary psychology because it assumes that the mind has been shaped by adaptive problems, which over time has resulted in mental adaptations to handle these problems (Tooby & Cosmides, 2015). It is a cognitive approach in the sense that it focuses on multiple aspects of how the brain processes information: perception, encoding, and decision-making. Furthermore, it encompasses both implicit, reflexive, cognitive processes and explicit, more flexible, cognitive processes (Maner et al., 2003). In addition, it takes a fundamental motives approach to cognition (Kenrick et al., 2010; Schaller et al., 2017) by investigating how a specific motivational state, in this case, related to mate choice, results in functional cognitive biases or attunements. From a Tinbergian perspective (Tinbergen, 1963), the approach is mainly concerned with identifying mechanistic explanations while assuming a functional basis. Maner & Ackerman (2015) discuss multiple examples related to different aspects of mate choice motivation and cognition. They discuss how people who look for a partner are more sensitive to cues of attractiveness (Maner et al., 2003), how differential reproductive costs for men and women result in sex differences in overestimating sexual interest (Haselton & Buss, 2000; Samara et al., 2021), and how being in a relationship results in lower sensitivity to attractive conspecifics (e.g., Karremans et al., 2011). In this dissertation, I will mainly focus on the first topic: how does mating motivation relate to cognitive attunement towards attractiveness or attractive traits?

This thesis addresses this research gap by investigating the interplay between cognition and mate choice in humans and Bornean orang-utans (*Pongo pygmaeus*). From a fundamental perspective, orang-utans are an interesting taxon to study this topic for two reasons. First, they are characterised by male bimaturism, meaning that adult males come in two distinct phenotypes (Utami et al., 2002). Second, orang-utan females seem to clearly prefer one type of male over the other when it comes to mating (Knott et al., 2009). From a practical perspective, the captive orang-utan population has relatively low breeding success (Kaumanns et al., 2004), and identifying cognitive tasks that can help to identify preferred mates could potentially help refining the orang-utan breeding programme.

To comparatively investigate the interplay between cognition and mate choice, both humans and Bornean orang-utans took part in various computerized tasks, eye-tracking studies and auditory playback setups. Additionally, humans were asked to provide attractiveness ratings of conspecifics, and went on speed-dates designed to resemble the natural mate choice context as much as possible (Finkel & Eastwick, 2008). Across different empirical studies, I investigated how immediate attention, voluntary attention and preferences were modulated by ratings of attractiveness (humans) or presence of secondary sexual characteristics (orang-utans).

Overall, the aim of this thesis is two-fold: to investigate to what extent attractiveness affects human cognition by employing different test paradigms, and to explore whether we can extend these paradigms to a closely-related great ape species. Such a comparison between related species will not only result in deeper understanding of the evolutionary emergence of cognitive phenomena (Panksepp et al., 2002; Smith et al., 2018), such as mate-related cognitive biases, and how they relate to socio-ecological differences between species, but the results of this thesis could also inspire practical applications, such as test paradigms that can identify individual mate preferences of zoo-housed animals. To start, I first provide an introduction to several concepts that are key to this thesis, after which I will provide an overview of the main themes discussed in this thesis.

Sexual selection and the evolution of attractiveness

From a biological perspective, evolved mate preferences are likely the result of sexual selection. In *The Descent of Man* (1871), Charles Darwin proposed his theory of sexual selection to explain the evolution of exaggerated secondary sexual characteristics, which are common in the animal kingdom. Darwin defined sexual selection as selection on "*the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction*" (Darwin, 1871, p. 256). Sexual selection can generally be divided into two types: intersexual selection, where traits make an individual more attractive to the opposite sex, and intrasexual selection, where traits are useful in competition between members of the same sex for access to mates. The sex that exerts these different types of sexual selection depends strongly on parental investment (Trivers, 1972), with females typically investing more energy in reproduction, leading to male-male competition and female choice. However, in species with biparental care, such as humans, mutual mate choice might be more common (Courtiol et al., 2016), because both sexes invest valuable energy in caring for their offspring.

Darwin's ideas about sexual selection remain remarkably relevant to current research (Jones & Ratterman, 2009). More specifically, his work has inspired many to apply sexual selection theory to the topic of attractiveness (Grammar et al., 2003; Rhodes, 2006). Such evolutionary theories of attractiveness rely on two main assumptions. First, attractiveness, or attractive characteristics should reflect an individual's ability to provide benefits either directly or indirectly (Jones & Ratterman, 2009). For example, an attractive individual might offer *direct benefits* to a partner (e.g., a good territory or defense against intruders). Alternatively, attractiveness might reflect *indirect benefits*, meaning that high levels of attractiveness correspond to genetic quality. Second, evolutionary theories assume that selecting attractive individuals as a partner is adaptive, because it might affect the number, health, or attractiveness of offspring (Grammer et al., 2003; Little, Jones, et al., 2011). Thus, attractiveness should reflect the quality of the partner, which in turn might affect the quality and/or quantity of offspring.

Both of these assumptions can be relatively easily tested in non-human animal species. For instance, in non-human primates, several examples of potentially attractive traits can be found. First, symmetry of either the face or the whole body has been hypothesized to indicate stable development, thereby serving as an indicator of genetic quality (Gangestad et al., 1994; Little, Jones, et al., 2011). In line with this, facial symmetry positively correlated with health and body condition in chimpanzees (*Pan troglodytes*: Sefcek & King, 2007) and rhesus macaques (*Macaca mulatta*: Little et al., 2012). Second, many male primates are characterized by secondary sexual characteristics preferred by females or associated with more reproductive output. For example, male gorillas (*Gorilla gorilla gorilla*) with more prominent sagittal crests, larger bodies, and larger gluteal muscles tend to have more mates and more offspring, reflecting female preferences for extreme sexual dimorphism (Breuer et al., 2012). Third, in some species, males show dynamic changes in appearance. Such changes in appearance often covary with competitive ability or health (reviewed in Petersen & Higham, 2020), and can covary with female preferences (e.g., Setchell, 2005). Thus, in line with the first assumption of evolutionary theories of attractiveness, specific male characteristics can be predictive of male quality, and might be preferred by females.

An overwhelming amount of evidence supports the second assumption, that selecting attractive individuals should result in healthier and/or more offspring. Most studies investigating this topic used a mate preference test to identify preferred mates. In this test, individuals are placed in a mate preference arena (e.g., Anderson et al., 2007; Pogány et al., 2014). These arenas allow an individual to inspect multiple conspecifics of the opposite sex. Based on different criteria, such as proximity, affiliative behavior, courtship behavior, and agonistic behavior, the preference of the chooser can be assessed. In most studies, half of the choosers are then paired with their preferred mate, while the other half is paired with a non-preferred mate. A qualitative review across taxa that examined results from such setups showed that quantitative and qualitative measures of reproductive output were almost exclusively higher for animals that were allowed to choose their partner (Martin-Wintle et al., 2019). This suggests that selecting individuals based on attractive traits might indeed facilitate successful reproduction.

Concluding, studies on non-human animals provide evidence for the assumption that attractive traits might inform conspecifics about mate quality, and that selecting for attractive traits might increase reproductive success. This raises the question of whether these assumptions also hold for humans.

Human mate choice

When considering evidence for both assumptions in human populations, a more complex pattern emerges. With regard to the first assumption, a clear link between visual attractiveness and markers of health has not been established yet: while some studies claim a positive association (Hönekopp et al., 2004; Mengelkoch et al., 2022; Nedelec & Beaver, 2014), other studies found null results (Cai et al., 2019; Jones et al., 2021; Pátková et al., 2022). When looking at specific traits that are considered attractive, a similar pattern emerges. A clear example of this is facial symmetry: humans rate symmetrical faces as more attractive (Rhodes, 2006) and healthy looking (Rhodes et al., 2007). It has also been suggested that symmetry might be a reliable indicator of health (Valen, 1962). However, studies have mostly failed to identify such a relationship (Hönekopp et al., 2004; Pound et al., 2014; Rhodes et al., 2001). It is important to note that these null results only show that the association between health and attractiveness is unclear in our *current* environment. A potential explanation for these equivocal findings is that health and attractiveness were related in our evolutionary past, but that this association has been obfuscated by recent innovations, such as modern medicine and beauty products (Thornhill & Gangestad, 1999). Altogether, there is no unequivocal evidence for a link between attractiveness and health in current human populations.

With regard to the second assumption, attractive humans seem to have more reproductive success, although the results are somewhat equivocal and the underlying mechanisms remain poorly understood. Some studies report a positive association between attractiveness and proxies of reproductive success, such as number of sexual partners (Rhodes et al., 2005), sexual activity (Karraker et al., 2017), probability of marriage (Prokop & Fedor, 2011), and number of offspring (Jokela, 2009; Pflüger et al., 2012; Prokop & Fedor, 2011). However, other studies report no association. For example, Sorokowski et al. (2017) found no significant difference in reproductive success between arranged marriages and non-arranged marriages in three indigenous societies, and Silva et al. (2012) even found a negative association between attractiveness and reproductive success in one population. Altogether, these results suggest that attractiveness and reproductive success are linked in humans, but the results are somewhat inconsistent.

One potential reason for the inconsistent findings on the topic of attractiveness and reproductive success is that human mate choice is a multifaceted phenomenon. One can imagine human mate choice as an enormous jigsaw puzzle, with attractiveness being just one of the pieces. To better understand the role of attractiveness in human mate choice, I will consider human mate choice as a two-stage process (Dixson, 2012; Fisher, 1998; Figure 1). When two potential mates meet, they will first judge each other on easily observable cues. This first stage can be considered an initial filter, and is especially driven by fast perception and appraisal of attractiveness (Dixson, 2012). Passing this first filter is required for *attraction* (Fisher, 1998). Ample evidence indeed shows that humans employ such a first filter when choosing a partner (Asendorpf et al., 2011; Eastwick & Finkel, 2008; Luo & Zhang, 2009; Sidari et al., 2021). Consequently, this first filter is also where we expect *sexually selective cognition* (e.g., or attention, memory, and implicit associations) to play a large role.

The importance or threshold of the first filter may differ between individuals. For instance, previous research has suggested that men and women might differ in the strength of their initial attraction-filter. More specifically, differential evolutionary costs are at play for men and women, resulting in different priorities during mate choice (Buss & Schmitt, 1993). One common conclusion from cross-cultural studies is that men value attractiveness more than women, while women put a stronger emphasis on resources (Buss, 1989; Li & Meltzer, 2015). While some studies indeed find indications of sex differences in cognitive biases towards attractiveness (e.g., Maner et al., 2003; Mitrovic et al., 2018; Zhang et al., 2017), this effect does not always replicate in ecologically valid studies of human mate choice, such as speed-date paradigms, were attractiveness is a good predictor of mate choice for both men and women (Eastwick & Finkel, 2008; Luo & Zhang, 2009; Selterman et al., 2015). Thus, while the attraction-filter may somewhat differ between men and women, the results are far from conclusive.

Only when a potential mate "passes" the first filter, the second filter will be applied. This filter corresponds to *attachment* (Fisher, 1998), and focuses more on perception and appraisal of personality traits and behavioural compatibility, and explicit judgements about a potential partner (Dixson, 2012). Attachment filters might be especially common in pair-bonding species like humans, where compatibility and behavioural coordination are essential for successful reproduction (Eastwick et al., 2023; Roth, Samara, Tan, et al., 2021). Concluding, from a temporal perspective, humans first "filter" their potential partners based on attractiveness, only after which they consider other factors, such as personality and behavioural alignment.

Although the second filter might be especially relevant for pair-bonding species, a first filter based on perception of attractiveness and the associated cognitive biases should also be present in other species. Therefore, in addition to investigating the influence of attractiveness on cognitive mechanisms in humans, this thesis will also investigate whether this is the case for Bornean orang-utans.

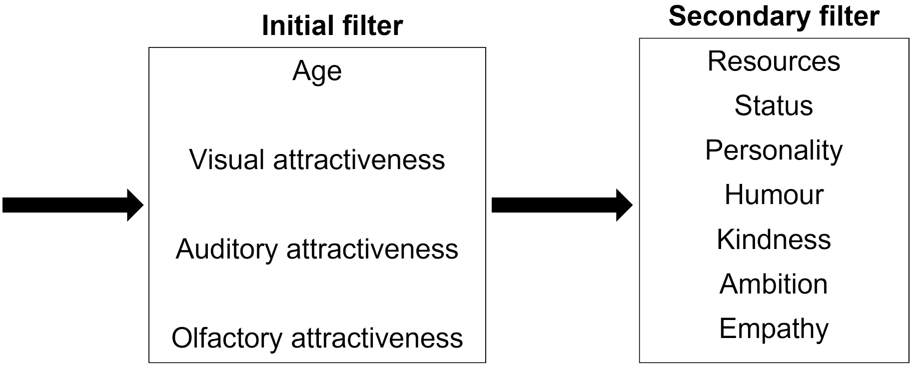

Figure 1. Schematic depiction of a two-stage model of human mate choice. Adapted from Dixson (2012).

Orang-utan socio-ecology

Orang-utans (*Pongo* spp.) are arboreal great apes that are native to Borneo and Sumatra. They share a last common ancestor with humans, that lived approximately 14 million years ago (Goodman et al., 1998). Currently, three species of orang-utans are distinguished (Figure 2): Bornean orang-utans (*P. pygmaeus*), Sumatran orang-utans (*P. abelii*) and Tapanuli orang-utans (*P. tapanuliensis*). Even though differences in behaviour can be found between different orang-utan species (Delgado & Schaik, 2000; van Schaik et al., 2008), recent work has emphasized their similarities (van Noordwijk et al., 2018) and suggests that some of the behavioural differences might result from plastic responses to local fruit availability (Roth et al., 2020). In general, orang-utans are characterized by a semi-solitary lifestyle, which is unique among the great apes (Mitra Setia et al., 2008; Roth et al., 2020; van Schaik, 1999). However, occasional social interactions do occur, and provide opportunities for socializing, playing, and mating (van Schaik, 1999). In some populations, the frequency of socialization seems linked to the availability of fruit, with more social interactions occurring during times of abundance (Roth et al., 2020).

Besides their peculiar social system, orang-utans are characterized by another uncommon trait, namely *male bimaturism*. This means that adult male orang-utans can be categorized in two distinct morphs: unflanged males and flanged males (Utami et al., 2002). Unflanged males experience a period of arrested development. They are sexually mature and can produce offspring, but are non-preferred mates for adult females (Knott et al., 2009; Kunz et al., 2022). In contrast, flanged males have fully developed secondary sexual characteristics, such as an extremely large body size, long hair, a large throat sac, and conspicuous flanges on the sides of their faces (Kunz et al., 2022). Furthermore, flanged males can produce long calls that seem to have a dual function: coordinating distance between males and attracting females (Mitra Setia & van Schaik, 2007). Importantly, orang-utan females seem to apply an *attraction filter* during mate choice: they prefer to mate with flanged males during their ovulation, potentially reflecting selection for good genes (Knott et al., 2009). Thus, the two male morphs are easily distinguishable based on visual and auditory cues, and females seem to discriminate between the morphs during their fertile phase.

Because orang-utans are characterized by two distinct male morphs, they provide an excellent species to study the interplay between secondary sexual traits and attention. While we know that secondary sexual characteristics affect cognitive processes such as attention in humans (Garza & Byrd-Craven, 2023; Yang et al., 2015), this topic has been virtually unexplored in great apes. However, to develop a full understanding of the evolutionary underpinnings of such attentional biases, it is important to test a wide range of species (Smith et al., 2018), ideally with different mating systems (Petersen & Higham, 2020). Because orang-utans are a suitable model organism for this topic, part of this thesis investigates whether Bornean orangutans show cognitive biases towards flanged males.

Figure 2. Pictures of flanged males of each orang-utan species. Left picture: courtesy of Ronald van der Beek. Middle picture: Tom Roth. Right picture: Tim Laman (redistributed under CC BY 4.0).

Dissertation outline

This dissertation consists of one review chapter and six empirical research chapters that investigate the influence of attractiveness or attractive traits on cognitive mechanisms that underly mate choice in either humans or orang-utans. The thesis is divided into three sections and a general discussion. Section 1 (Chapter 2) presents a literature review summarizing experimental paradigms that are relevant to the thesis. Section 2 (Chapters 3-5) provides evidence for biased visual attention towards attractive conspecifics in humans. Section 3 (Chapters 6-8) investigates visual attention and preference towards flanged males in Bornean orang-utans (*Pongo pygmaeus*). Chapter 9 concludes this thesis with a general discussion. I want to emphasize that, while the chapters are logically ordered in this thesis, most of them were performed in parallel. Based on the pattern that emerges from the chapters, I have placed them in a logical order. Furthermore, because the chapters were written as independent research articles, they contain some theoretical overlap.

Chapter 2 provides a theoretical basis for the empirical chapters, by reviewing previous research that investigated how attractiveness modulates cognition in humans and cognitive biases towards attractive characteristics in primates. Furthermore, I discuss test paradigms that can potentially be used to study mate preferences in primates, some of which will be used in the empirical chapters, and I discuss the practical relevance of applying such tasks to refine zoo breeding programmes.

Chapter 3 examines the role of visual, auditory and olfactory attractiveness in human mate choice, using a naturalistic speed-date paradigm and attractiveness rating tasks. The main aim of this chapter was to investigate the notion that human attraction is multimodal, by comparing the relative importance of visual, auditory and olfactory attractiveness on willingness to date again.

Taking into account the results of Chapter 3, **Chapter 4** specifically focuses on visual cognition by investigating how immediate attention and reflexive gaze cueing in humans are modulated by general ratings of facial attractiveness, and facial symmetry, a trait that is often associated with attractiveness. The goal of this chapter is to test whether attractiveness-driven implicit cognitive biases exist in a community sample, irrespective of idiosyncratic attractiveness preferences. Furthermore, we explored whether such biases were driven by sex and age.

Chapter 5 follows up on this work by not relying on pre-defined attractiveness categories, and taking idiosyncratic preferences into account instead. By combining cognitive tasks, attractiveness rating tasks, and speed-dating, I explore to what extent immediate and voluntary visual attention are driven by idiosyncratic attractiveness preferences, and how they relate to human mate choice in a speed-date context.

Chapter 6 is the first chapter that moves away from humans. Here, I apply cognitive tasks to measure immediate attention and preference to investigate whether zoo-housed Bornean orang-utans have an immediate attentional bias towards flanges and symmetrical faces, and a choice bias for pictures of flanged males. To study this, I used two well-established computerized task: the dot-probe task to study immediate attention, and a preference test to study choice bias.

Chapter 7 extends this work by testing Bornean orang-utans using a non-invasive eye-tracking setup, similar to the setup that was used to test humans (Chapter 5). Across two experiments, I explored whether orang-utans showed biased immediate and voluntary attention towards flanged males. Furthermore, the design of the second experiment allowed to explore whether the orang-utans showed a stronger attention bias towards certain conspecifics.

In **Chapter 8,** the thesis shifts its focus from visual to auditory information by investigating the effect of orang-utan long calls on female behaviour. More specifically, I describe two case reports of ovulation-induced vocalization and behavioural sensitivity towards male long calls in female Bornean orang-utans. These two cases suggest a potential role for male long calls in orang-utan female mate choice. Furthermore, these cases are the first to indicate that female orang-utans might produce ovulation vocalizations that communicate their proceptivity.

Finally, **Chapter 9** closes the thesis with a general discussion and conclusion, where I emphasize and integrate the main findings from this thesis, and compare my findings in humans and Bornean orang-utans. I also propose relevant directions for future research and discuss practical applications.

Chapter 2

“I go bananas for you”: Extending sexually selective cognition to non-human primates

Abstract

Recent psychological research has suggested an important role for cognitive processes in human mate choice. The extent to which a person is attractive has a strong influence on whether humans attend to this person, remember their face, or are motivated to keep watching them. Despite the flourishing research on primate cognition in recent years, studies examining sexually selective cognition in primates are still relatively scarce. However, a better comparative understanding of sexually selective cognition is important to gain better understanding of the evolutionary processes underlying the attractiveness biases we observe in humans. Furthermore, existing techniques for evaluating sexually selective cognition in primates could have practical applications for conservation breeding programs by allowing for identification of individual mate preferences. In this review, we therefore discuss evidence for sexually selective cognition in humans and the scant work in primates, adopting a comparative perspective. Based on our review, we suggest experimental paradigms that can be used to study sexually selective cognition in primates, and the potential application of these paradigms to inform conservation breeding programs. We emphasize that beyond informing our evolutionary understanding of the interplay between mate choice and cognition, studying sexually selective cognition in primates can help improve well-being and potentially increase reproductive success in captive primates.

Based on:

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Introduction

Choosing a mate is one of the most critical decisions that animals make during their life: selecting a suitable mate can result in a good representation of the individual's genes in the next generation, whereas selecting an unsuitable mate might result in the loss of your genes from the population. Consequently, the selective pressures associated with searching for a mate profoundly influence the evolution of cognition (Maner & Ackerman, 2015; Miller & Todd, 1998). We can clearly observe this effect in humans: when asking people to describe how they feel about their loved one, or how they felt when they first met, they often refer to specific cognitive processes such as attention, memory, and implicit associations. "I could not get my eyes off of her" or "I cannot get him out of my head": such statements are typical when referring to a preferred romantic partner. Evidence from psychological studies shows that these statements are not misguided when they imply that attraction has a significant cognitive component.

More specifically, cognitive processes may be sensitive to traits that are relevant for mate choice. Due to the strong incentive to choose a suitable mate, mate choice is guided by multiple signals and cues that might reflect the quality of a potential mate (Andersson, 1994; Candolin, 2003). Accordingly, many species have evolved preferences for these traits (Darwin, 1871; Manson, 2011). More specifically, primate males often bear variant and invariant traits that are preferred by females or associated with higher reproductive output (Lüpold et al., 2019). These traits can be indicators of either direct benefits that the male can offer, such as protection, or indirect benefits, such as high genetic quality (Paul, 2002). An example that already captivated Charles Darwin is the male mandrill (*Mandrillus sphinx*). Darwin contended that *"[n]o other member of the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill"* (Darwin, 1871, p. 292), and suggested that the bright coloration of the males is probably attractive to females, something that we now know is indeed the case (Setchell, 2005).

Although ultimate questions regarding mate choice in non-human primates (hereafter, primates) have been studied extensively, the interaction between primate cognition and mate choice remains unclear. In humans, by contrast, a plethora of studies has shown that information that is relevant for mate choice affects human social cognition; several cognitive processes, such as attention and memory, are attuned to physical attractiveness (Maner & Ackerman, 2015).

For example, humans selectively attend to attractive faces, memorize them differently than unattractive faces, and work harder to see attractive faces. These cognitive biases towards indicators of mate quality (e.g., facial attractiveness; Little et al., 2011) have been termed as *sexually selective cognition* (Maner & Ackerman, 2015).

While many studies have explored this topic in humans, only a limited number of studies have examined it in primates with mixed results. Although an evolutionary approach has already been successful in gaining an understanding of the relationship between mate choice and cognition in humans, a full understanding of the evolution of sexually selective cognition requires a comparative approach. Typically, a comparative approach to cognition involves identifying differences in cognitive traits across multiple species, and then seeking to explain these differences by examining relevant factors, such as ecological and social variables (MacLean et al., 2012; Vonk & Shackelford, 2012). For instance, Amici et al. (2008) have used such an approach to show that measures of social complexity correlate positively with inhibitory control in primates. When considering sexually selective cognition, we can obtain better insight into how sexual selection shapes cognition by investigating whether factors such as mating system and ornamentation explain variance in cognitive biases towards potential mates.

This fundamental knowledge is interesting in itself, but importantly, some of the methods to test sexually selective cognition in primates might have practical applications in conservation breeding programs. Currently, most programs do not incorporate mate preferences, but instead they strongly rely on pedigree information (Asa et al., 2011). However, recent studies have established that allowing free mate choice is associated with increased reproductive output (Martin-Wintle et al., 2019). Interestingly, many of the paradigms that can be employed to study sexually selective cognition from a fundamental perspective, can theoretically be used to identify individual mate preferences as well. Most importantly, these methods could be applied to test for mate preferences despite the fact that individuals are housed at distant locations. If this is indeed the case, breeding recommendations could be refined by not only pairing individuals with a genetically suitable conspecific, but in addition also taking into account their individual mate preferences. This could potentially increase well-being of captive primates and ultimately also reproductive success.

In this review, we argue that studying sexually selective cognition in primates has both fundamental and practical benefits, and that researchers should employ recent technological developments to elucidate the interaction between sexual selection and cognition. The review is divided into three sections. First, we review the literature on sexually selective cognition in humans. Second, we review the scant literature on sexually selective cognition in primates. Third, we suggest paradigms suitable for studying sexually selective cognition in primates and discuss the application of such paradigms in a broader context.

Sexually selective cognition in humans

Sexually selective cognition can be defined as the cognitive processes or biases that facilitate mating-related goals. Such goals can vary, from identifying potential competitors to avoiding threats to existing relationships. However, the most crucial steps in mate choice may be identifying and evaluating suitable mates. Previous studies have shown that human cognitive processes are sensitive to attractiveness (Maner & Ackerman, 2015). Here, we discuss how attractiveness relates to different aspects of human cognition by considering the effect of attractiveness on visual attention, recognition memory, and motivational processing. It should be noted that our review of the human literature is not exhaustive. Instead, we aim to provide a general overview of the findings.

Visual attention

Individuals encounter more information in their environment than they can process at any given moment. Visual attention mechanisms aid in selectively perceiving relevant information from the environment and filtering irrelevant information (Dukas, 1998; Krupp, 2008). From an evolutionary perspective, it is reasonable to assume that attentional mechanisms are specifically sensitive to evolutionarily relevant information related to opportunities and dangers in the environment (Cosmides & Tooby, 2013). Accordingly, humans selectively attend to fitness-relevant information such as emotional expressions (Carretié, 2014) and animate objects (New et al., 2007). Since finding a mate is possibly the best example of searching for opportunities in the environment, multiple studies have tried to elucidate the role of attractiveness in human social cognition by studying how visual attention is biased towards attractive conspecifics. Altogether, it is reasonable to expect that humans selectively attend to attractive conspecifics (Krupp, 2008; Lindell & Lindell, 2014).

Selective attention involves three main components: engagement, disengagement, and attentional shifting (Blicher et al., 2020; Posner & Petersen, 1990). While engagement refers to the start of selective attention to a stimulus, disengagement refers to the termination of attention to a specific stimulus. Disengagement can be followed by shifting attention and engaging with another stimulus (Blicher et al., 2020; Koster et al., 2006). Importantly, attentional biases can manifest in multiple components of selective attention. For example, threatening stimuli might receive preferential engagement (Carretié, 2014) and, at the same time, be more difficult to disengage from (Cisler & Koster, 2010). Furthermore, attentional biases can become apparent in preferential looking designs, in which people can voluntarily attend to different stimuli within a certain timeframe (Winters et al., 2015). These designs do not test a specific component of attention but instead allow participants to engage, disengage, and shift attention multiple times. In this section, we discuss whether people have attentional biases towards attractive faces specifically with regard to (1) engagement, (2) disengagement, and (3) voluntary attention.

Engagement

To navigate our romantic environment, it is essential to focus on attractive conspecifics. Accordingly, research indicates that human attention is immediately captured by attractive faces. For instance, people can detect the location of attractive stimuli above chance accuracy, even when the images are shown for only 100 ms (Guo et al., 2011), and the presentation of attractive faces as distractor stimuli for 100 or 200 ms results in lengthened task performance in a spatial cueing task (Sui & Liu, 2009). Furthermore, studies with longer presentation times (300 ms) have shown that participants attend more to attractive faces than to unattractive ones, irrespective of participants' age and sex (Roth et al., 2022). Nevertheless, another recent study did find indications for a sex difference in engaging with attractive stimuli: men's reaction times, but not those of women, were influenced by their individual attractiveness preferences (Roth et al., 2023). This highlights that research into sex differences in immediate attention is still inconclusive. In summary, while humans tend to preferentially engage with attractive faces, more research is needed to understand how demographic factors such as age and sex influence this bias.

A slightly subtler pattern emerges from eye-tracking studies on the attentional engagement of erotic and attractive stimuli. Fromberger et al. (2012) studied initial fixation in heterosexual men and found that participants were more likely to fixate on pictures of women than on pictures of men. However, this bias did not generalize to pictures of boys and girls, suggesting that this immediate attentional bias was present only in the context of sexually relevant stimuli. Subsequently, Dawson & Chivers (2016, 2018) presented pairs of female and male stimuli to participants. Their results extended these finding by showing that heterosexual men are more likely to fixate on women than men. However, interestingly, their findings showed that women fixated equally frequently on men and women, suggesting that they do not exhibit the same bias as men. Thus, men and women seem to exhibit different patterns in attentional engagement when using more sensitive measures, such as eye-tracking.

Moreover, using a similar paradigm in which target photographs displayed two same-sex stimuli differing in attractiveness, Leder et al. (2016) found no difference in the proportion of first fixations landing on the most attractive face. This was also the case in a paradigm in which attractive and unattractive faces were embedded in real-world scenes (Leder et al., 2010). Thus, findings from eye-tracking studies suggest that attractive stimuli may not immediately capture attention, which differs from the results obtained from computerized tasks. Altogether, although men's attention seems to be captured by female stimuli, the attractiveness of the depicted individuals does not seem to affect the initial fixations.

Disengagement

Do attractive faces hold attention? Studies examining this question seem to converge on the finding that humans have trouble disengaging from attractive faces. In general, these studies employ a cuing task: a picture is presented in the center of the screen (500 ms) and then replaced by an object in one quadrant of the screen. Participants need to indicate the shape of the object by pressing a corresponding key. If a stimulus holds attention, people are expected to respond slower on the key press task.

Using this approach, Maner et al. (2007) found that sexually unrestricted participants, who were more promiscuous and more open to casual sex, disengaged slower from stimuli that depicted attractive opposite-sex faces using a dot-probe task. Similarly, a series of studies with a Chinese sample using a slightly different version of the task showed that single women (Ma, Zhao, et al., 2015) and men (Ma et al., 2019) had trouble disengaging from attractive opposite-sex faces. In line with these findings, Zhang et al. (2017) found a similar bias among singles using attractive and unattractive bodies in an attentional disengagement task. Thus, attractiveness seems to hold attention and impede attentional disengagement among single participants.

It should be noted that most of the aforementioned studies found a delayed disengagement effect only after participants were primed with either romantic words or words related to mate choice. Moreover, most studies found delayed disengagement from attractive faces only in single participants. This concords with the notion that top-down control plays an important role in attentional disengagement (Theeuwes, 2010). More specifically, individual mating motivations can modulate attentional disengagement: when individuals are motivated to look for a mate (e.g., through priming mating motivation), they will be slower to disengage from attractive faces. Conversely, if participants are motivated to retain an existing relationship, they will disengage more quickly from attractive faces, regardless of the priming condition.

Voluntary attention

When examining the impact of attractiveness on attention over a longer time span, eye-tracking studies have consistently shown that humans tend to gaze longer at sexually preferred or attractive stimuli. Typically, these studies employ a preferential looking paradigm in which two images are presented simultaneously while participants' eye movements are tracked. Dawson & Chivers (2016) conducted a study that involved presenting participants with sexually explicit pictures and videos of same-sex and opposite-sex individuals. Their results indicated that heterosexual men and women fixated more on static opposite-sex stimuli. However, when using video stimuli in which two opposite-sex individuals were present, they found that men fixated more on the opposite-sex stimulus, whereas women exhibited a same-sex bias (Dawson & Chivers, 2018). Thus, while previous research has established that heterosexual men generally show an opposite-sex bias, the pattern for women is more complex and nuanced.

Another line of inquiry focuses on how specifically attractiveness influences voluntary attention. For example, Mitrovic et al., (2016) examined whether attractiveness influences voluntary attention as a function of participants' sexual orientation by presenting participants with naturalistic stimuli (i.e., everyday scenes containing facial stimuli). The researchers presented homosexual and heterosexual men and women with pairs of faces depicting either their preferred or non-preferred sex, which varied in attractiveness. Their findings revealed that participants exhibited an attentional bias toward attractive faces but only when the stimuli matched their preferred sex. Although this study pre-classified pictures as attractive or unattractive, subsequent studies employed stimuli with a wider range of attractiveness ratings and incorporated individual attractiveness ratings instead of pre-classification (Leder et al., 2016; Mitrovic et al., 2018; Roth et al., 2023). In general, more recent studies presented combinations of stimuli with a wide range of attractiveness and asked participants to rate the stimuli for attractiveness on a 1 to 7 scale. Subsequently, they found that the difference in attractiveness score between the two simultaneously presented stimuli was positively correlated with the difference in looking time, suggesting that the larger the difference in attractiveness, the stronger the bias toward the attractive face (Leder et al., 2016; Mitrovic et al., 2018). Moreover, participants, who were in this case all heterosexual, were especially attentive to attractive faces of the opposite sex (Mitrovic et al., 2018), in accordance with the idea that mate search motives partly shape voluntary attention.

The effect of mate search motives on voluntary attention is further supported by the finding that relationship status seems to modulate this effect. Leder et al. (2016) suggested that the correlation between looking time and attractiveness was more robust for single participants than for those in a relationship. In a follow-up study, Mitrovic et al. (2018) confirmed this pattern, as single participants who were more interested in casual sex exhibited a stronger positive correlation between attractiveness ratings and attentional bias than participants in a committed relationship or those who were more sexually restricted. This is in line with a sexual selection explanation, given that single people, particularly those motivated to find a partner, should be more attentive to opportunities in their environment. Moreover, a recent study among single heterosexual adolescents combined a preferential looking task with attractiveness ratings and speed-dating, and found that participants not only had an attentional bias towards attractive opposite-sex faces, but also towards pictures of people they wanted to date, although this effect could be driven by the correlation between attractiveness rating and willingness to date (Roth et al., 2023). Nevertheless, these results highlight the potential link between attentional biases and mate choice.

In short, studies on voluntary attention reveal that males tend to prefer looking at opposite-sex pictures, whereas both males and females tend to prefer looking at attractive opposite-sex individuals. Additionally, relationship status and sexual (un)restrictedness appeared to modulate this effect. Taken together, the results of these studies reveal the important role attention plays in mate selection.

Recognition memory

From an evolutionary perspective, it is important not only to perceive salient social cues from faces but also to memorize attractive faces as remembering attractive individuals may help guide behaviour during recurrent interactions (Avery et al., 2016) or in comparative evaluation of facial cues (Bateson & Healy, 2005). Several studies have investigated the effects of attractiveness on recognition memory. Typically, such studies first present participants with a series of faces that differ in attractiveness. After a brief interval, participants are presented with a new series of images, consisting of novel as well as previously presented stimuli, and are asked to indicate for each image whether they have seen the face before (Wiese et al., 2014).

The findings of these studies are mixed. While some studies report enhanced memory for only attractive faces (Lin et al., 2020; Marzi & Viggiano, 2010; Tsukiura & Cabeza, 2011; Zhang et al., 2011), other studies report the opposite effect, namely that participants memorize unattractive faces more accurately (Wang et al., 2016; Wiese et al., 2014), or find no effect of attractiveness on recognition memory (Wickham & Morris, 2003). One potential reason for this discrepancy is that distinctive faces are more likely to be stored in memory. Because average faces are considered more attractive (Jones & Jaeger, 2019; Valentine et al., 2004), unattractive faces might be more likely to stand out in a set of attractive and unattractive faces, thus facilitating their subsequent retrieval from memory. However, one study controlled for the effect of distinctiveness and still found better recognition memory for unattractive faces (Wiese et al., 2014). Nevertheless, this example highlights the need for careful methodology and disentangling of correlated facial characteristics in future studies.

Other factors also influence how memorable a face is, for example, the sex of the target face and perceiver. Some findings show that people preferentially remember attractive female faces compared to average female, male, and attractive male faces (Becker et al., 2005). In contrast, other studies suggested that women remember attractive male faces, but men show no such bias (Allan et al., 2012; but see Wang et al., 2016). Similarly, a recent study (Lin et al., 2020) showed that perceiver age moderates the relationship between attractiveness and memory. Specifically, younger participants showed a more substantial memory bias for attractive faces compared to less attractive faces of young people, whereas older participants did not show this bias. From an evolutionary perspective, this is not surprising, as young adults are in the period of their lives where they experience the most sexual attraction. Therefore, memory bias for attractiveness in this age group would benefit mate choice. However, the moderating effects of demographic variables such as age and sex on recognition memory of attractive faces remain equivocal and require further investigation.

An intriguing line of research has examined the effect of attractiveness on decision-making processes using signal detection theory. Interestingly, humans demonstrated more false alarms, meaning that they indicated that they recognized a face that was not previously presented, when the face was attractive than unattractive (Silva et al., 2016; Wang et al., 2016; Wiese et al., 2014). According to Silva et al. (2016), this false recognition bias can be adaptive because it results in increased salience of attractive people. With the idea that they have already seen attractive people, humans may be more likely to consider attractive people as suitable partners, even if they have not seen or met them before. Although this may sound like an appealing adaptive explanation, more parsimonious explanations should be considered. For example, as mentioned above, it could also be a by-product of the distinctiveness of unattractive faces. Nevertheless, poorer recognition accuracy for attractive faces seems to persist even when controlling for distinctiveness (Wiese et al., 2014). Alternatively, it could be argued that a more accurate memory of unattractive faces will help to avoid these in the future. This suggestion is in line with the idea that humans do not have a positive association with attractive faces per se, but seem to have a negative association with unattractive faces (Griffin & Langlois, 2006). However, this adaptive explanation remains untested, and based on current evidence, it seems that the apparent false recognition bias could indeed be driven specifically by attractiveness, even though the adaptive benefit of such a bias remains tentative.

Altogether, the effect of attractiveness on recognition memory remains equivocal, as some studies suggest improved recognition accuracy for attractive faces, whereas others suggest the opposite. Although adaptive explanations have been proposed for both findings, there is still no clear consensus regarding the underlying mechanism. Furthermore, the roles of facial distinctiveness, sex, and age require further attention to obtain a better understanding of the interplay between attractiveness and recognition memory.

Effort

In addition to attentional and memory processing, some studies have investigated the motivational drive elicited by attractiveness by measuring how much effort people exert to see attractive faces. Building on the idea that the desire to achieve a goal and the emotional response when accomplishing it are distinct processes, Berridge & Robinson (2003) formulated a theory that integrates the neurological and psychological components of motivation. They distinguish between the desirability of reward and the emotional experience of reward, where desirability is defined by the extent to which a particular reward is desired ("wanting"), and emotional experience refers to the subjective experience of pleasure or pain ("liking"). While "wanting" is expressed via the mesolimbic dopamine system, "liking" is expressed via opioid hotspots (Berridge & Kringelbach, 2015). This theory has also been applied to the study of attractiveness; while "wanting" can be tested by employing an effort task, "liking" is reflected in explicit ratings of attractiveness (Levy et al., 2008).

Typically, participants who engage in an effort task can control the presentation duration of a picture by pressing specific keyboard keys. More specifically, they can choose to increase or reduce how long they view a specific image by exerting effort through pressing the corresponding keys. If they work to *increase* the presentation duration of an image, this image has a high motivational salience. In a seminal study, Aharon et al. (2001) combined an effort task with attractiveness ratings and functional brain imaging. The authors found that men exerted effort to look longer at attractive female faces but not attractive male faces. In line with the behavioral responses, viewing attractive female faces was associated with increased activation of the nucleus accumbens, a brain area associated with rewards (Berridge & Kringelbach, 2015).

Extending these findings, Hayden et al. (2007) examined the influence of participants' sex on the relationship between attractiveness and effort. The authors recruited both male and female participants and presented them with a series of opposite-sex faces that ranged in attractiveness. Their results showed that although men and women exerted more effort to see attractive than unattractive opposite-sex faces, the effect was significantly stronger for male participants. Crucially, this study only presented participants with opposite-sex pictures. Therefore, a similar study presented same-sex and opposite-sex pictures to participants and found that only men showed an opposite-sex bias for attractive faces in the effort task, while women exerted more effort to see attractive same-sex and opposite-sex pictures. In addition, the amount of effort exerted by males to see attractive females was substantially higher than that exerted by females for attractive faces (Levy et al., 2008). Thus, motivational salience seems to depend on the interaction effect among participant sex, stimulus sex, and stimulus attractiveness.

In conclusion, these studies demonstrate that men and women are willing to exert effort to view attractive individuals. However, while men are specifically motivated to watch opposite-sex individuals, women do not show a sex-related bias in effort. These findings illustrate a discrepancy between "liking" and "wanting" in men. Specifically, men rate attractive males and females as more attractive than unattractive males and females but will work only to view attractive females. For women, on the other hand, "liking" and "wanting" seem to be more positively associated than for men, as women exert effort to see both attractive males and females (Levy et al., 2008). Thus, there seems to be a sex difference in the motivation to see attractive faces.

Sexually selective cognition in primates

While sexual selection and mate choice have been widely studied in primates (e.g., Dixson, 2012; Paul, 2002), relatively few studies have investigated how mate choice is related to cognitive processes, such as memory, attention, and motivation. To date, sexually selective cognition in primates has mostly been studied through preferential looking experiments (Winters et al., 2015). In these experiments, individuals are confronted with different types of pictures presented either sequentially or simultaneously during a trial. In the case of sequential presentation, the visual preference can be deduced from the average attention in trials showing picture type 1 vs. the average attention in trials showing picture type 2. In the case of simultaneous presentation, visual preference becomes apparent when looking at the attention relative to each picture. This method has not only been used in the context of mate choice, but has also elucidated the effects of familiarity (Hanazuka et al., 2013; Lewis et al., 2021) and emotions (Pritsch et al., 2017; Roth et al., 2023; van Berlo et al., 2023) on visual attention.

Most primate studies on mate choice and visual attention have focused on macaques (Supplementary Table 1). Seminal work by Waitt and colleagues showed that rhesus macaque (*Macaca mulatta*) females have an attentional bias towards bright red male faces when they were paired with paler male faces (Waitt et al., 2003), while males seemed to have a preference for bright red female hindquarters, but not faces (Waitt et al., 2006). Similarly, macaques seem to be biased towards symmetrical faces (Waitt & Little, 2006). Such biases might be adaptive during mate choice, because factors such as symmetry or coloration are thought to reflect the mate quality or fertility of the bearer.

More recent work has been based on these previous studies. For instance, Higham et al. (2011) showed that free-ranging rhesus macaque males on the island of Cayo Santiago showed a bias towards the faces of ovulating females when they were paired with faces of the same female from a non-ovulatory period. Interestingly, this bias became especially apparent when males were presented with pictures of familiar females, suggesting that familiarity could affect the perception of mate-relevant information. Other studies in Cayo Santiago revealed a bias for red faces (Dubuc et al., 2016) and masculine faces (Rosenfield et al., 2019). In addition, Pflüger et al. (2014) found that Japanese macaque (*Macaca fuscata*) males show a bias towards bright red female faces when paired with paler versions of the same face. Furthermore, recent macaque studies have investigated bias for averageness, with mixed results (Damon, Méary, et al., 2017; Tomeo et al., 2017), and it has been established that macaques show an own-species bias for attractive faces, similar to humans (Damon et al., 2019). Thus, many studies have successfully utilized the preferential looking paradigm to study selective attention toward secondary sexual characteristics.

Only a handful of studies have applied this paradigm to primate species other than macaques. Cooper & Hosey (2003) used a sequential paradigm with different lemur species and found that in common brown lemurs (*Eulemur fulvus*), which are characterized by sexual dichromatism (i.e., the difference in colour between the sexes), females showed an attentional bias towards more brightly coloured males. No such bias was found in the control group, which consisted of lemurs that did not experience sexual dichromatism. This suggests that the coloration of common brown lemurs might be sexually selected through female choice. In addition, two studies investigated attentional biases in capuchin monkeys. Paukner et al. (2017) studied whether male and female capuchin monkeys (*Cebus apella*) had an attentional bias for symmetrical male and female faces. They only found a symmetry bias for males seeing male faces, suggesting that males use facial symmetry to judge the quality of competitors. Second, Lonsdorf et al. (2019) investigated whether capuchin monkeys were biased towards same-sex or opposite-sex conspecifics. They found that females looked longer at same-sex stimuli, whereas no clear bias was found in males. Altogether, preferential looking tasks have been successfully applied to study mostly macaque species, even though a few studies have extended this method to other species.

In addition to preferential looking tasks, some studies have used different test paradigms to investigate preferences for secondary sexual characteristics. Deaner et al. (2005) developed a *pay-per-view* paradigm in which rhesus macaques could give up a certain amount of their reward to look at pictures depicting different conspecifics. They found that individuals were willing to give up rewards to look at high-status faces and the perinea of conspecifics. Watson et al. (2012) adapted the paradigm into a free-ranging version. On a touchscreen, female rhesus macaques could choose between two coloured dots, one of which they had learned to associate with an empty screen and one with a specific image category during forced-choice trials at the start of the session. Irrespective of their choice, individuals received a reward at the end of each trial. By changing the image category between sessions, the authors identified the image categories that were most preferred over seeing an empty screen. Based on their choices, female macaques seemed to prefer pictures of perinea and high-status faces, confirming the results of Deaner et al. (2005). Thus, it seems that rhesus macaques choose to look at stimuli that contain traits indicative of good mate quality when they are “asked” what they want to see.

In short, studies of sexually selective cognition in primates have mostly focused on attention and choice tasks. Furthermore, the range of species that have been tested is very narrow. Therefore, future studies should not only employ a wider range of paradigms encompassing different cognitive processes but also apply them to a wider range of species.

Opportunities for sexually selective cognition research in primates

As shown in this review, many different paradigms have been used to examine sexually selective cognition in humans, but relatively few have been employed in primates, even though some would be suitable for this purpose. Therefore, we suggest specific methods that can be employed in future primate research. Many of these methods have already been used to study other topics such as emotions and categorization abilities. Similar to the section on sexually selective cognition in humans, we separated this section into three subsections: attention, memory, and effort.

Attention

Recent studies have employed the dot-probe paradigm to measure immediate attention in primates (MacLeod et al., 1986; see van Rooijen et al., 2017 for a review). In this paradigm, two stimuli appear on a touchscreen for a brief moment, one of which is subsequently replaced by a dot that needs to be clicked. If an individual's attention was already attracted to the picture that was replaced by the dot, they would click the dot faster. However, if their attention was focused on the other image, they would first need to shift their attention before they could touch the dot, which would result in a slower reaction time. Using this method, researchers have investigated emotional cognition in bonobos (Kret et al., 2016; van Berlo et al., 2023), chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018), orang-utans (Laméris et al., 2022), macaques (King et al., 2012; Lacreuse et al., 2013) and capuchin monkeys (Schino et al., 2020). Given that humans show a bias for attractive faces in the dot-probe paradigm (Roth et al., 2022, 2023), it could be worth exploring whether primates have similar biases in this paradigm. Importantly, it is possible to investigate both attentional engagement and disengagement using the dot-probe paradigm (Koster et al., 2004). Therefore, the dot-probe paradigm can potentially be used to develop a fine-grained view of attentional biases towards attractive conspecifics.

Alternatively, one could investigate whether certain stimuli receive more attention using eye-tracking. As outlined earlier in this review, many studies on primate sexually selective cognition have used preferential looking paradigms. In many of these studies, researchers videotaped the responses of primates to stimuli and later scored their gaze direction and attention duration. However, such measures are relatively crude and require intensive analysis of the video materials. Recent developments in eye-tracking techniques allow the collection of precise and accurate data regarding primate attention (Hopper et al., 2021). Some of the studies mentioned previously have already employed eye-tracking to investigate primate sexually selective cognition (Damon et al., 2019; Lonsdorf et al., 2019). Still, a more elaborate use of this technology could aid our understanding of primate sexually selective cognition. While many studies have used eye-tracking to investigate topics such as attention to emotions (Pritsch et al., 2017), the effect of familiarity on attention (Lewis et al., 2021), theory of mind (Krupenye et al., 2016), and memory (Kano & Hirata, 2015) in great apes, no eye-tracking studies have systematically investigated sexually selective cognition. Future studies could further explore this line of research.

Memory

To date, only one study has explicitly investigated memory for mate-relevant stimuli in primates. Lacreuse et al. (2007) presented rhesus macaque females with a delayed recognition span task at different points during their menstrual cycle, where they had to memorize the faces of conspecific males or females. In this task, individuals need to identify new stimuli in a grid that contains an increasing number of stimuli. For instance, the grid first contains one stimulus that the individual needs to click on to obtain a reward. Next, a second stimulus appears on the grid, and the individual obtains a reward only if they click the new stimulus in the grid. This process proceeds until the individual makes a mistake. Interestingly, the authors found no difference in recognition memory for male and female faces, and this effect did not change across the menstrual cycle. However, the overall accuracy was not significantly higher than chance level, which suggests that the task may not be the most appropriate way to study memory for faces in primates.

An additional paradigm that can be used is the delayed match-to-sample task, which has been applied to investigate working memory (Lind et al., 2015) and categorization abilities (Vonk, 2013). In this paradigm, individuals first see a sample image they need to click to start the trial. After a short delay, two (or more) images appear on the screen, one of which is similar to the sample image. Selecting this “correct” image results in a reward for the individual. Vonk (2013) has employed this paradigm to investigate species categorization abilities in orangutans, showing that they can rapidly learn to match images depicting similar species. Employing this approach, it would be possible to test whether primates can better memorize pictures that contain mate-relevant cues. If they reach higher accuracy in trials where they are presented with pictures that contain indicators of high mate quality, this may indicate an enhanced memory of such information.

Effort

When it comes to effort, a few more studies have investigated this topic in primates. Often, these tasks are based on the presentation of videos. By pressing on the screen, individuals can control the duration of the video so that exerting more effort (e.g., holding their finger on the screen for a longer time) results in a longer presentation of the video fragment. In general, videos function as a reward, so individuals receive no food reward for participation. Tsuchida & Izumi (2009) used this method to study video preference in Japanese macaques and found that individuals pressed longer when the video on the screen depicted monkeys. A similar study on Japanese macaques found a preference for videos depicting humans or animations (Ogura & Matsuzawa, 2012). Thus, effort paradigms have been developed and are relatively easy to apply in non-human primates.

Effort tasks can be used to study the evolution of sexually selective cognition in primates. For instance, by presenting individuals with videos and measuring the effort they invest to keep watching videos that contain mating information versus non-mating information, researchers can investigate whether primates are motivated to access information relevant to mate choice. If they are, follow-up studies could present primates with videos that contain indicators of good mate quality versus less attractive physical features. Consequently, researchers can test whether primates have an increased motivation to watch stimuli that contain information associated with good mate quality. Such studies can offer valuable insights into how sexual selection shapes cognition in primates.

Future applications: sexually selective cognition and conservation breeding

Successful reproduction of zoo-housed animals is essential for zoos to fulfil their conservation goals. Conservation breeding involves the careful management of captive animal populations to promote population growth or stability while at the same time preserving genetic variation. To achieve these objectives, captive populations must maintain a healthy age and sex structure, genetic diversity, and avoid inbreeding. To this end, conservation breeding programs rely mostly on pedigree information to suggest appropriate breeding recommendations (Briscoe et al., 2002). For example, individuals with low mean kinship (i.e., low relatedness to the captive population) may be preferentially selected for breeding to ensure that genetic diversity is optimized within the population. However, these breeding assignments are often not fulfilled. In general, only approximately 20% of breeding recommendations result in offspring (Cronin et al., 2006; Faust et al., 2019), and this number may be even lower in species with a long generation length (Faust et al., 2019). One potential explanation is that "couples" that seem to be a good match based on pedigree information, do not always prefer each other as mates. Therefore, we suggest that conservation breeding programs should employ computerized tasks to identify mate preferences and incorporate these into their breeding recommendations.

Recent studies have suggested that conservation breeding programs should try to incorporate mate preferences when formulating breeding assignments (Asa et al., 2011; Martin & Shepherdson, 2012; Martin-Wintle et al., 2019). By incorporating such preferences, the probability of mate incompatibility can be reduced, thereby increasing reproductive output. Recent studies have convincingly shown that allowing animals to choose their mates can increase reproductive success (Martin-Wintle et al., 2019). This conclusion is based on studies using a lover's lane setup, in which an individual can inspect multiple potential mates. By scoring the behaviour of the chooser (e.g., affiliation), researchers can identify the preferred mate of the chooser (Martin-Wintle et al., 2019). For instance, Martin-Wintle et al. (2015) investigated the relationship between mate choice and reproductive success in giant pandas (*Ailuropoda melanoleuca*). They measured mate preferences by allowing pandas to interact with multiple opposite-sex individuals in adjacent enclosures. Based on their behaviour, they formed free mate choice pairs and control pairs, and found that allowing for free mate choice was associated with higher reproductive success. Thus, incorporating mate preferences can increase pairing success and reproductive output.

However, this lover's lane setup is not suitable for all zoo-housed animals (e.g., great apes), as their future mates are typically housed at distant locations. Therefore, the development of practical long-distance methods to reliably test mate preferences is essential (Asa et al., 2011). Further research on sexually selective cognition in primates might be helpful in practical terms. By developing reliable methods that can measure preferences and biases for specific individuals or individual characteristics, it would be possible to measure individual mate preferences to some extent before an individual is transferred to a new zoo. This approach may potentially increase the success of the introduction and reproductive success.

To the best of our knowledge, no studies to date have employed visual tasks to this effect, although similar approaches have been used to study the role of smell in conservation breeding (Fisher et al., 2003; Mossotti et al., 2018). However, we suggest that conservation breeding programs attempt incorporating some of the paradigms we have discussed. The goal here is not to replace the current method of matching based on pedigree information but to add an extra filter in the case of multiple suitable matches. For instance, if two males are both suitable for pairing with a female for breeding, researchers could investigate whether the female has a measurable preference for one male over the other. By employing an effort task, they can test whether the female will work more to see videos of one male over the other, while a preferential looking task could elucidate whether the female selectively attends to one of the males. We expect that incorporating such information will help refine breeding recommendations.

Admittedly, sexual selection in primates extends beyond their sensitivity to visual information. For instance, vocalisations and olfactory signals are also important for mate choice in primates and humans. Other authors have extensively discussed these topics in both primates (vocalisation: Delgado, 2006; olfaction: Drea, 2015) and humans (vocalisation: Puts et al., 2014; olfaction: Mahmut & Croy, 2019). Similarly, a large body of research on sexual selection in primates concerns copulatory and post-copulatory mechanisms, such as sperm competition and cryptic female choice (Dixson, 2018). Although these modalities and processes are essential for primate evolution, diurnal primates are well adapted to processing visual information (Barton, 1998; DeCasien & Higham, 2019). Therefore, we focused specifically on visual tasks.

Furthermore, species-specific traits, such as a species' mating system, may be strongly associated with the suitability of the proposed approach. For instance, visually conspicuous traits that are relevant for mate choice are especially common in polygynous primate species, whereas they are less common in monogamous or promiscuous species (Dixson, 2012; Dixson et al., 2005). In addition, for monogamous species with biparental care, mate preferences are expected to strongly relate to behavioural compatibility (Baxter et al., 2023; Florkiewicz et al., 2018), because a couple that is behaviourally compatible will also have a better chance of raising offspring successfully (Roth, Samara, Tan, et al., 2021). Thus, the approach proposed here initially appears to apply mostly to polygynous species.

In conclusion, although the study of sexually selective cognition in primates is interesting from a fundamental perspective, it may also have practical applications. Currently, most conservation breeding programs do not consider individual mate preference. We propose that the computerized tasks discussed in this review can address this issue as they can be employed as long-distance methods to identify mate preferences in primates. However, it is important to note that this approach may not be equally suitable for all species. Furthermore, future research should establish whether incorporating long-distance measures of visual mate preferences translates into improved introduction success or reproductive output in captive primates. If such a link can be established, this could lead to significant improvements in the management of captive breeding programs and the conservation of endangered primate species.

Conclusion

In this review, we suggested that the study of sexually selective cognition should be extended to primates and proposed test paradigms for this effect. Our scientific understanding of the interplay between attractiveness and human cognition has advanced significantly in recent years owing to extensive research employing a range of different paradigms and encompassing different cognitive processes such as attention, memory, and motivational processing. Taken together, these studies have shown that some cognitive processes in humans are sensitive to facial attractiveness. These results fit well with an evolutionary approach to cognition: attractiveness plays a pivotal role in human mate choice; therefore, sensitivity to environmental cues of attractiveness can aid in finding or evaluating a potential mate.

Although research on primate cognition has thrived in the past decades, relatively few studies have investigated sexually selective cognition in primates. Therefore, we suggest that multiple paradigms used to study cognition in primates could also be employed to study sexually selective cognition. This is important for two reasons. First, from a fundamental perspective, testing multiple primate species will provide better insight into how sexual selection shaped cognition. Second, from a practical perspective, we believe that some of the test paradigms can be used to identify the individual mate preferences of captive primates. By incorporating such preferences, conservation breeding programs can improve the well-being of captive primates and, ultimately, their reproductive success.

Chapter 3

Multimodal mate choice: Exploring the effects of sight, sound, and scent on partner choice in a speed-date paradigm

Abstract

When people meet a potential partner for the first time, they are confronted with multiple sources of information, encompassing different modalities, that they can use to determine whether this partner is suitable for them or not. While visual attractiveness has widely been studied with regard to partner choice, olfactory and auditory cues have received less attention, even though they might influence the attitudes that people have towards their partner. Therefore, in this study, we employed a combination of pre-date multimodal rating tasks followed by speed-date sessions. This offered a naturalistic setup to study partner choice and disentangle the relative effects of a priori attractiveness ratings of sight, scent and sound on date success. Visual attractiveness ratings showed a strong positive correlation with propensity to meet the partner again, while the effects of olfactory and auditory attractiveness were negligible or not robust. Furthermore, we found no robust sex differences in the importance of the three modalities. Our findings underscore the relative importance of visual attractiveness in initial mate choice, but do not corroborate the idea that static pre-date measures of auditory and olfactory attractiveness can predict first date outcomes.

Based on:

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/5VLTJ0.

Introduction

Choosing a partner is an extremely important decision, not only because a good relationship is one of the main predictors for a happy life (Soons et al., 2009), but also from an evolutionary perspective. Selecting a suitable partner might result in healthy offspring; whereas, a wrong choice might result in loss of fitness (Buss & Schmitt, 2019). However, humans typically lack explicit knowledge about the quality of potential partners when meeting them for the first time. This raises the question of how people distinguish between preferred and non-preferred mates based on brief interactions (Kurzban & Weeden, 2005). Evolutionary-based theories posit that humans evolved partner preferences for physical traits that are indicative of mate quality, such as facial attractiveness, sound of voice, and olfactory pleasantness (Grammer et al., 2003). Therefore, humans might initially filter potential partners on the basis of these traits and then only select the suitable individuals (Dixson, 2012; Fisher, 1998). Here, we investigated how different sensory modalities influence this initial filtering by combining a naturalistic speed-dating event with multimodal rating tasks to disentangle the effects of scent, facial attractiveness, and the attractiveness of the voice on dating success.

It is well known that attractive humans experience numerous benefits in human societies. For example, individuals that are considered attractive might receive a more positive evaluation of their personalities, have higher chances of being hired for a position, and tend to go on more dates than less attractive people (Little, Jones, et al., 2011). Interestingly, visual attractiveness seems to transcend cultural boundaries, as people from different cultures seem to largely agree on attractiveness ratings (Langlois et al., 2000). Not only do people agree on what is attractive, but visual attractiveness is central in human mate choice for both men and women (Buss & Barnes, 1986; Rhodes, 2006). Previous research has shown that facial attractiveness predicts female and male attraction to a partner (Feingold, 1990; Luo & Zhang, 2009), also in speed-date settings (Asendorpf et al., 2011; Sidari et al., 2021). It has been suggested that choosing an attractive partner might help to ensure offspring with good quality, as different aspects of facial attractiveness may indicate optimal health or genetic quality (Rhodes, 2006; but see Foo et al., 2017). Thus, visual attractiveness is an important part of human mate choice.

Visual input is not the only information humans perceive when selecting a mate. On the contrary, recent evidence suggests that attractiveness is multimodal, and voice and scent also influence mate choice decisions (Havlíček et al., 2008; Mahmut & Croy, 2019; White & Cunningham, 2017; Groyecka et al., 2017). Humans can efficiently extract information about a person's identity and current state from a voice, such as female ovulatory status (Bryant & Haselton, 2009; Puts et al., 2013), emotional state (Belin et al., 2008), male physical dominance (Hodges-Simeon et al., 2010; Sell et al., 2010), body size (Wheatley et al., 2014), and age (Skoog Waller et al., 2015). When it comes to voice qualities and voice attractiveness, multiple aspects seem to affect what is considered an attractive voice. For example, women tend to prefer lower-pitch voices (masculine voices), while men prefer higher-pitch voices (feminine voices), and both men and women prefer averaged voices. Importantly, these general preferences do seem to differ between individuals; suggesting that what is an attractive voice for one person, might not be attractive for the other (Pisanski & Feinberg, 2018; Vukovic et al., 2010, 2011). This finding highlights the importance of accounting for individual preferences when examining partner choice. Even though people can identify attractive voices from recordings, vocal attractiveness is also affected by the dynamics during an interaction, such as changes in voice pitch (Pisanski et al., 2018) and vocal convergence (Farley et al., 2013). Thus, whether attractiveness ratings of isolated vocal samples predict date success remains to be examined.

Not only the voice, but also the scent of a potential partner might be used as a cue when it comes to partner choice (Havlíček et al., 2008; Mahmut & Croy, 2019; White & Cunningham, 2017). Importantly, humans use scent to extract an impressive amount of information relevant for mate choice, such as sex, dominance, fertility, health, and genetic compatibility (Groyecka et al., 2017; Lobmaier et al., 2018; Roberts et al., 2008). Interestingly, smell might be more important for women than for men (Havlíček et al., 2008). Previous research on olfactory preferences of men have mainly focused on genetic compatibility (e.g., Roberts et al., 2008) and ovulatory shift effects (e.g., Lobmaier et al., 2018), while the contribution of olfactory attractiveness in male mate choice has remained relatively unexplored. Altogether, these findings suggest that incorporating vocal and olfactory cues of attractiveness might explain a substantial amount of variance in mate choice.

Despite the plethora of studies on attractiveness and partner choice, the question of how the different modalities of attractiveness relate to one another remains equivocal. From an adaptive point of view, the different modalities can either convey the same information (*back-up cue hypothesis*), or convey different information (*multiple message hypothesis)* about an individual (Candolin, 2003). Thus, according to the *back-up cue hypothesis,* multimodal cues might all reflect the same underlying mate quality, which would result in a more accurate assessment of mate quality. Alternatively, the *multiple message hypothesis* assumes that multimodal cues might each reflect different aspects of mate quality. Taken together, these cues reflect overall mate quality; however, each multimodal cue reflects a different *component* of this quality (Candolin, 2003; Johnstone, 1997). For humans, multiple studies have suggested that different modalities covary in signaling underlying mate quality. For example, both vocal and facial characteristics correlate in women (Collins & Missing, 2003), and may be used to assess hormonal status (Feinberg, 2008), and ratings of facial attractiveness and olfactory attractiveness concord in both men and women (Cornwell et al., 2004). This suggests that the different modalities might indeed reflect the same qualities in humans.

Traditionally, studies have investigated the role of scent, sight and sound by means of isolated experiments in which participants rated multiple static samples for attractiveness and long-term partner suitability. Consecutively, these ratings are often linked to traits of the sampled individual, such as masculinity and femininity (Collins & Missing, 2003; Cornwell et al., 2004; Little, Connely, et al., 2011). However, it has not yet been established how these individual ratings relate to real-life partner choice. In our study, we combined these widely-used multimodal attractiveness ratings of static stimuli with a speed-date paradigm. Speed-dates are a useful tool to study social decision making, as they allow for experimental control, while at the same time offering high ecological validity (Finkel et al., 2007). Thus, by combining pre-date multimodal rating tasks with consecutive speed-date outcomes, the current study explores whether pre-date attractiveness ratings of the different modalities correlate with willingness to meet again after a speed-date. Our study especially explores three main topics, namely (i) how do pre-date attractiveness ratings of different modalities relate to each other, (ii) is attraction indeed multimodal, and (iii) do men and women differ when it comes to the importance of the different modalities?

Methods

Participants

Eighty participants were recruited through online advertisement and flyering at the university buildings for a scientific speed-dating event in Leiden, The Netherlands. Seventy (N = 70) attended the experimental session (35 women, M_{age} = 22.03, SD = 2.14; men: M_{age} = 22.49, SD = 1.97). Twenty-two women used hormonal contraceptives. In line with the inclusion criteria, all participants reported that they were between 18 and 26 years old, heterosexual, single, Dutch-speaking, and not under treatment for psychiatric disorders. Furthermore, all participants reported normal or corrected-to-normal vision and normal color vision, as well as normal hearing acuity. Three participants (1 woman) dropped out before the speed-dating part of the study; resulting in a final sample of 67 participants and 277 speed-dates. All participants provided informed consent as according to the declaration of Helsinki. Participants were not compensated for their participation, but received a ticket to Apenheul Primate Park (Apeldoorn, the Netherlands) to thank them for their participation. The procedure and methods were approved by the Leiden University Ethics Committee (CEP: 2020-02-20-M.E. Kret-V1–2169).

Procedure

The experiment (pre-registered using the AsPredicted database, reference number: #36394) took place on the 28th of February and 1st of March 2020 in Leiden, The Netherlands. In the 4 weeks before the experiment, participants signed up via an online Qualtrics form (Qualtrics, Provo, UT), where they selected a specific time to participate in the experiment (i.e. selected their group). Each group consisted of a maximum of 10 men and 10 women. Participants were instructed that prior to their arrival they avoid wearing heavy make-up, strong-smelling products (e.g., perfume and deodorant), and provocative clothing.

Upon arrival to the experimental session, men and women were seated in different rooms and were asked to provide informed consent, and fill in questionnaires regarding background information (e.g., education, use of dating apps) and trait sexual desire (Elaut et al., 2010; Spector et al., 1996). After participants completed the questionnaires, a researcher took a standardized portrait picture separately for each participant using a Canon EOS 40D camera set at portrait mode, with a EF 28-135 mm f/3.5–5.6 IS USM lens. The photographer was located 1 m from the participant, and zoomed in so that a slight empty space was present around the face of the participant. For this picture, participants were asked to pull their hair back, remove their glasses, remove large pieces of jewelry, and display a neutral facial expression. The photographs were not edited further.

The audio stimuli were recorded in a separate sound-proof room. A researcher recorded audio stimuli separately for each participant. Participants were asked to read out loud the Dutch equivalent of the RAINBOW passage (Van Lierde et al., 2001) using a Shure MV5 microphone set at flat mode (i.e., no equalization or compression) and Audacity® (sample rate:44.1 kHz). Participants were instructed to sit approximately 30 cm away from the microphone, and to speak with normal pace, volume, and tone. If the participant made a mistake while reading the text, the recording was repeated from the start. Stimulus collection occurred in parallel for men and women, and lasted approximately 1 h.

In addition, each participant brought a worn t-shirt which was used as olfactory stimulus. To standardize the preparation of the olfactory stimuli, we asked participants to wear the t-shirt during the night before the experiment, and put it in a closed plastic bag in the morning. Furthermore, we asked them to follow specific guidelines (Roberts et al., 2008) before and during wearing the t-shirt: a) not use perfumed products; b) avoid excessive consumption of alcohol and tobacco; c) not consume spicy foods; d) refrain from sexual activity; e) sleep alone.

Following stimulus collection, participants performed six cognitive tasks, three of which were the rating tasks for sight, sound, and scent (see below). The task-related section of the experiment lasted approximately 1 h. Thereafter, all participants were asked to proceed to the speed-date room, where they had a maximum of 10 speed-dates. The speed-dating phase of the study lasted for a maximum of 1 h. After the end of the experiment, participants were thanked for their participation, received a zoo ticket, and were debriefed.

Rating tasks

In all rating tasks, participants rated the stimuli on a 1–7 scale. First, they answered the question “How attractive do you find this person’s face/voice/scent?”. Second, they answered the question “How suitable do you find a person with these looks/this voice/this scent as a long-term partner?”. For all three modalities, the rating tasks were presented on a desktop computer via *E*-Prime 3.0 (Psychology Software Tools, Pittsburgh, PA). Participants could rate the stimuli by using numeric keys 1 to 7. Stimulus order was randomized for all participants. In addition, the task order was randomized, so that not all participants rated the different modalities in the same order.

To measure facial attractiveness and vocal attractiveness, participants rated 10 opposite-sex pictures and 10 opposite-sex audio fragments on attractiveness and long-term partner suitability. The stimulus set consisted of the stimuli gathered from the 10 opposite-sex participants in the same timeslot. If the number of opposite-sex participants was lower than 10, extra stimuli of participants from another timeslot were added to make sure that the number of trials was the same for all participants. The pictures were presented for 3 s on a computer monitor, while presentation duration of the audio recordings was equivalent to their duration (±20 s). Participants used a Logitech H340 USB Headset to listen to the audio recordings.

To measure olfactory attractiveness, we used the t-shirts that participants prepared at home. After arrival, each t-shirt was placed in a glass jar, that was numbered 1–10 (see Roberts et al., 2008). We wrapped all jars in black paper, so that participants could not see the visual features of the t-shirt. In each trial of the experiment, a random number between 1 and 10 appeared on the screen. A researcher, wearing surgical gloves, brought the corresponding jar to the participant and allowed the participant to smell the t-shirt and next rate the attractiveness of the scent (see above). However, there were two important differences compared to the visual and vocal rating task. First, participants could indicate that the scent was not strong enough to answer the question(s) by pressing the *0* keyboard key, to control for samples with extremely low intensity. Second, if the number of opposite-sex participants in a group was lower than 10, the remaining jars would stay empty. So the number of trials between groups and sexes could slightly differ for the olfactory task.

Speed-dates

In the speed-date room, men and women were seated 2 by 2 at opposite sides of a table. We made video recordings of both participants during each date, the content of which will not be further discussed in the present paper. Barriers were placed on the table to avoid that participants would interact before the date started. At the start of each date, participants were asked to rotate the barriers in front of them by 90 degrees, so that each table was divided into two “dating booths”. Thereafter, the start of the date was indicated by a ringing bell. After 4 min, the participants were asked to turn the barriers again and indicate a) how attractive they found their partner; b) how attractive they considered them as a long-term mate; c) whether they would be interested in going on another date with them; d) whether their partner would like to go on another date with them; e) whether they knew each other from before. Answers on questions a, b, and c were very strongly correlated (Supplementary Tables 1-2). Participants were given approximately 1 min to fill in the scorecard. After each date, men moved one seat to the left.

In each group, the number of speed-date rounds depended on the number of participants in each group per sex, with a maximum of 10 rounds. In addition, if the number of men and women was not equal, the overrepresented sex had one or multiple rounds without a speed-date. In total, the experiment consisted of 277 speed-dates, thus resulting in 554 filled-in scorecards.

Data processing

Because of technical issues, in the second female group (*N* = 8) we could not collect data for the vocal and visual rating task, and thus had to exclude them from further analysis. Second, one of the auditory stimuli that was used in the third female group did not match with the male in that group. Therefore, all data for the male whose auditory stimulus was missing was excluded from analysis. Third, one male in the second group did not complete the visual rating task. Fourth, we excluded all rows in which the participant had scored the olfactory rating with a 0, as this was an indication that the participant could not make a choice based on the sample.

After excluding the above-mentioned data, we first tested how strongly the attractiveness ratings correlated with long-term partner suitability ratings using Bayesian ordinal regressions (see Data Analysis). Because the two questions were always asked together, and in the same order, we suspected a carry-over effect, resulting in almost identical ratings for attractiveness and long-term partner suitability. This was indeed the case for all three modalities (Supplementary Tables 3–6). Because of the strong degree of correlation, we used only the attractiveness ratings in our further statistical analyses. We chose attractiveness ratings over long-term partner ratings because the former are more straightforward and align better with the relatively short-term context of a speed-date event. The full dataset based on the attractiveness ratings of all three modalities and speed-date outcomes included 457 complete cases after exclusion of data as described above. For the independent models, we used all complete cases of the specific modality (visual: 482, auditory: 481, olfactory: 533; Supplementary Table 7).

Data analysis

To analyse the data, we used Bayesian ordinal regression to test how the different modalities were correlated with each other, and Bayesian mixed models to explore whether attractiveness ratings were associated with speed-date outcome. All Bayesian models were created in the Stan computational framework and accessed using the **brms** package (Bürkner, 2017, 2018), version 2.13.5. In all analyses we centered ratings at 4, because this was the middle option. This was done to ease setting priors on the intercept. All models were run with 4 chains and 5000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van de Schoot, 2017). We found no divergences or excessive autocorrelation.

For the ordinal regressions, which allow the dependent variable to be of the ordinal type (Bürkner & Vuorre, 2019), we specified six models with a cumulative distribution, consisting of the attractiveness ratings for one modality as dependent variables, and attractiveness ratings of another modality as predictor. We added random intercepts for rater and rated individual, and allowed the slope of the predictor to vary by rater. Furthermore, we retained the default priors for the error terms and thresholds, and set conservative Gaussian priors with a mean of 0 and SD of 0.5 for the predictor.

To test the relationship between multimodal attractiveness and speed-date outcome, we used Bayesian mixed models with a Bernoulli distribution, with willingness to meet again (yes/no) as response variable. First, we conducted a partial correlation analysis, which contained visual, auditory and olfactory attractiveness each interacting with sex as predictors. Second, we used three independent models with either visual, auditory or olfactory attractiveness as predictor, interacting with sex. This allowed us to see how strong the correlations were per modality when not controlling for the other two modalities. Also, it allowed for a slightly larger sample size per modality, because there were more complete cases. We added random intercepts for participant and dating partner, and allowed slopes for the attractiveness ratings to vary by participant. With regard to priors, we set a conservative Gaussian prior with a mean of 0 and SD of 1 for the intercept. For the predictors, we used conservative Gaussian priors with a mean of 0 and SD of 0.5. For the error terms, we set half-Cauchy priors with a scale of 1.

We report multiple quantitative measures to summarize the posterior distribution. First, we report the median Odds Ratio (*MdnOR*) and median absolute deviation of the Odds Ratio (MAD) of the estimate. Second, we report a 89% credible interval of the Odds Ratio (89% CrI). We have chosen 89% instead of the conventional 95% to reduce the likelihood that our results are interpreted as strict hypothesis tests (McElreath, 2018). Instead, the goal of the credible intervals is to communicate the shape of the posterior distributions. Third, we report the probability of direction (*pd*), i.e. the probability of a parameter being strictly positive or negative, which varies between 50% and 100% (Makowski et al., 2019). Fourth, we report an approximation of Cohen's *d* (Borenstein et al., 2009).

Results

Correlation between modalities

We first explored whether the attractiveness ratings in the different modalities were correlated, using Bayesian ordinal regressions (Table 1, Supplementary Tables 8–10). We found that all modalities were slightly positively correlated. However, this relationship became most apparent for the correlations between visual and auditory, and visual and olfactory attractiveness, while the correlation between auditory and olfactory attractiveness was not as robust. Importantly, even for the former two findings, effect sizes were relatively small, indicating that the correlation between the modalities is not strong. Furthermore, estimates were very similar for men and women.

Table 1. Estimates and effect size measures for the concordance in attractiveness ratings between modalities. All estimates are based on ordinal regression models (see Supplementary Table 8–10).

Dependent	Predictor	Rater sex	*Median OR*	*CrI 89%*	*pd*	*d*	*N*
Visual	Auditory	Female	1.25 [0.15]	1.04; 1.52	0.97	0.12 [0.07]	473
Visual	Auditory	Male	1.27 [0.13]	1.08; 1.51	0.99	0.13 [0.06]	
Auditory	Visual	Female	1.30 [0.15]	1.09; 1.56	0.99	0.15 [0.06]	
Auditory	Visual	Male	1.38 [0.16]	1.15; 1.66	1.00	0.18 [0.06]	
Visual	Olfactory	Female	1.21 [0.12]	1.03; 1.42	0.97	0.10 [0.06]	465
Visual	Olfactory	Male	1.20 [0.12]	1.02; 1.40	0.96	0.10 [0.05]	
Olfactory	Visual	Female	1.24 [0.13]	1.04; 1.47	0.97	0.12 [0.06]	
Olfactory	Visual	Male	1.22 [0.13]	1.03; 1.46	0.97	0.11 [0.06]	
Auditory	Olfactory	Female	1.15 [0.11]	0.98; 1.34	0.92	0.08 [0.05]	465
Auditory	Olfactory	Male	1.13 [0.11]	0.97; 1.31	0.90	0.07 [0.05]	
Olfactory	Auditory	Female	1.20 [0.13]	1.00; 1.44	0.95	0.10 [0.06]	
Olfactory	Auditory	Male	1.12 [0.11]	0.96; 1.31	0.88	0.06 [0.05]	

Multimodal attractiveness and date outcome

Partial effects

To determine the relationship between multimodal attractiveness ratings and date outcome, we used a Bayesian mixed model with a Bernoulli distribution (Supplementary Table 11; Figure 1; see Appendix G for model stability checks). We found a robust positive association between visual attractiveness rating and date outcome, meaning that participants were more likely to indicate they wanted to go out again with individuals that they had rated as visually attractive (Figure 1). This pattern was apparent for both male (*MdnOR* = 3.09 [0.62], 89% CrI [2.31; 4.40], *pd* = 1.00, *d* = 0.62 [0.11]) and female (*MdnOR* = 2.25 [0.40], 89% CrI [1.71; 3.06], *pd* = 1.00, *d* = 0.45 [0.10]) participants. While the effect was slightly stronger for males, the difference between males and females was not robust (*MdnOR* = 1.38 [0.32], 89% CrI [0.96; 2.03], *pd* = 0.92, *d* = 0.18 [0.13]).

With regard to auditory attractiveness (Figure 1), we found a small positive association for males, suggesting that men were more likely to want to go on another date with women whose voices they rated as attractive (*MdnOR* = 1.31 [0.22], 89% CrI [0.99; 1.72], *pd* = 0.94, *d* = 0.15 [0.10]). For females, on the other hand, no robust pattern emerged (*MdnOR* = 1.17 [0.20], 89% CrI [0.89; 1.55], *pd* = 0.82, *d* = 0.08 [0.09]). In addition, we found no robust sex difference in the importance of auditory attractiveness (*MdnOR* = 1.12 [0.25], 89% CrI [0.78; 1.61] *pd* = 0.69, *d* = 0.06 [0.12]).

For olfactory attractiveness, however, we found an opposite pattern (Figure 1). For males, we found no clear directional effect of olfactory attractiveness on date outcome (*MdnOR* = 0.93 [0.14], 89% CrI [0.73; 1.18], *pd* = 0.69, *d* = 0.04 [0.08]), while we found a robust but small negative association for females (*MdnOR* = 0.73 [0.11], 89% CrI [0.57; 0.92], *pd* = 0.99, *d* = 0.17 [0.18]). This indicates that women were slightly less likely to want to meet again with men they rated as smelling attractive. While the effect for women was stronger than for men, the sex difference was not robust (*MdnOR* = 1.27 [0.25], 89% CrI [0.93; 1.75], *pd* = 0.89, *d* = 0.13 [0.11]).

Independent effects

Because some of the ratings showed some correlation between modalities, and visual attractiveness was such a strong predictor in the partial effects model, we also explored the correlation between attractiveness rating and date outcome using independent models per modality (Table 2; Supplementary Table 7). We

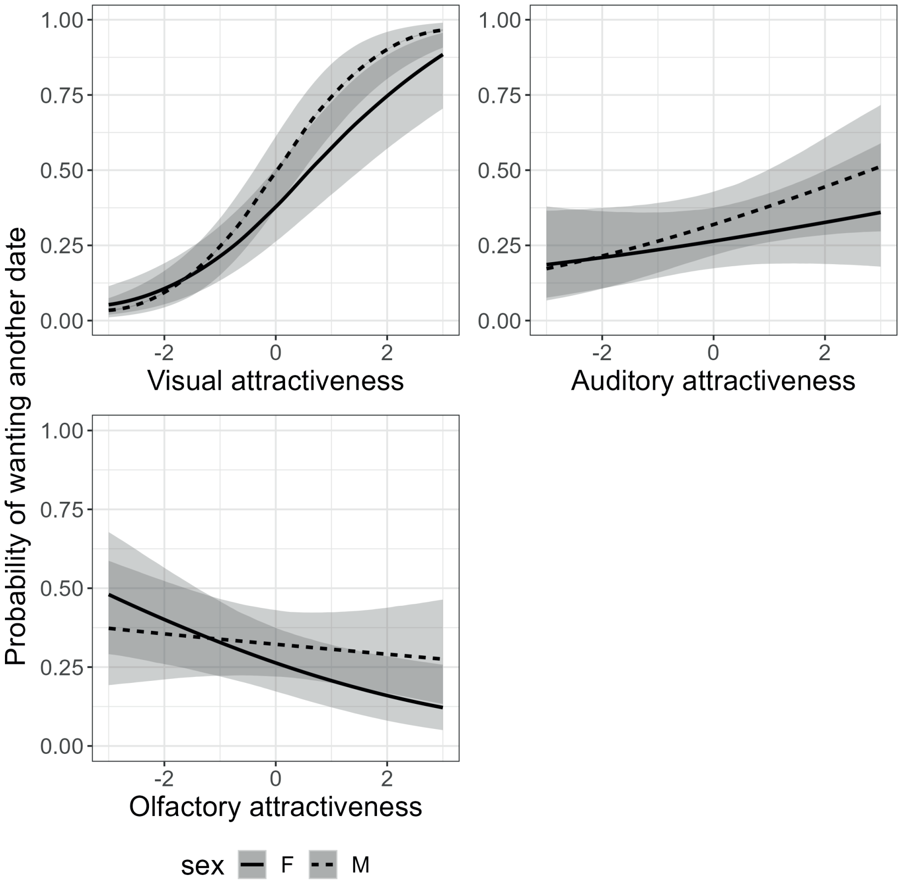

Figure 1. The relationship between visual,, auditory, and olfactory attractiveness ratings (centered), respectively, and probability of wanting another date for both male raters and female raters. Values are conditioned on the mean for the other predictors. Shaded areas show 89% Credible Intervals.

found that the relationship between auditory attractiveness and date outcome became slightly more apparent in the independent models for females. Furthermore, we found more robust sex differences in the visual context (i.e., visual attractiveness was more strongly correlated with date outcome for males than for females) and the olfactory context (i.e., a small negative correlation between olfactory attractiveness and date outcome for females, and no clear pattern for males). However, the independent models still indicated that visual attractiveness showed a strong positive correlation with date outcome for both men and women.

Table 2. Estimates and effect size measures for independent logistic regressions, separately testing the effect of attractiveness in each modality on propensity to date again (see Supplementary Table 7).

Modality	Rater sex	Median OR	CrI 89%	*pd*	*d*	*N*
Visual	Female	2.01 [0.31]	1.59; 2.61	1.00	0.39 [0.08]	482
Visual	Male	2.91 [0.50]	2.24; 3.92	1.00	0.59 [0.10]	
Visual	Interaction	1.45 [0.30]	1.04; 2.05	0.96	0.20 [0.12]	
Auditory	Female	1.26 [0.20]	0.98; 1.65	0.93	0.13 [0.09]	481
Auditory	Male	1.30 [0.20]	1.02; 1.67	0.96	0.14 [0.08]	
Auditory	Interaction	1.04 [0.21]	0.74; 1.44	0.55	0.02 [0.12]	
Olfactory	Female	0.82 [0.10]	0.66; 0.99	0.95	0.11 [0.07]	533
Olfactory	Male	1.08 [0.14]	0.88; 1.34	0.73	0.04 [0.07]	
Olfactory	Interaction	1.33 [0.23]	1.01; 1.76	0.95	0.16 [0.10]	

Discussion

Choosing a romantic partner is an important life decision. Previous research has mainly focused on the role of physical attractiveness during early stages of partner choice (Asendorpf et al., 2011; Kurzban & Weeden, 2005; Sidari et al., 2021). However, recent evidence reveals that attractiveness is multimodal, further involving scent and sound (Groyecka et al., 2017). Therefore, here, we examined the effect of multimodal attractiveness ratings of static samples in an ecologically valid speed-date setting (Finkel et al., 2007) and asked participants to indicate whether they would like to meet their dating partner again. To our knowledge, this is the first study that examines the effect of sight, sound and scent on speed-date outcomes. Our results are threefold. First, we show that there were only low levels of covariance in the different modalities of attractiveness. Second, using a partial model and independent models, we show that pre-date visual attractiveness ratings correlate strongly with propensity to meet again, while no strong effects were found for vocal and olfactory attractiveness. Third, in the partial model we found no robust sex differences in the importance of the different modalities. In the independent models, however, we did find robust sex differences for the effects of visual and olfactory attractiveness. Here, we discuss these findings and further address possible limitations of our study.

In the current study we observed that visual attractiveness correlated positively with auditory attractiveness and olfactory attractiveness, respectively. This finding is in line with the *back-up cue hypothesis* (Candolin, 2003; Johnstone, 1997). However, it is important to note that the effect sizes were very small when compared to previous studies (Collins & Missing, 2003; Cornwell et al., 2004), and it is therefore questionable whether such low correlations have any practical relevance. In addition, we did not find clear differences between sexes, while some of the previous studies only described such concordance of multimodal attractiveness ratings in a specific sex (e.g., Collins & Missing, 2003). Larger studies may be better suited to detect such nuances in future work.

Our most prominent finding is that, from all three modalities, facial attractiveness showed the strongest correlation with willingness to date again across both genders. This is in line with previous findings from speed-date paradigms (Asendorpf et al., 2011; Luo & Zhang, 2009), and experimental paradigms incorporating multimodal attractiveness ratings (Foster, 2008). This finding is not surprising, given that humans are extremely visually-oriented beings, rendering sight the most conspicuous source of information in mate choice (Krupp, 2008). Thus, our results corroborate the relative importance of facial attractiveness compared to scent and sound during initial phases of partner selection. Indeed, in a busy public place, such as a bar or a speed-dating event for that matter, visual information is the most apparent and reliable cue upon first acquaintance, because auditory cues might be distorted by noise and olfactory cues will be difficult to perceive in isolation (Thomas-Danguin et al., 2014), given the fact that mixing with other people's odour might obfuscate individual olfactory cues.

In line with this notion, we found little evidence to support the multimodal nature of attractiveness during speed-dates. Auditory attractiveness seemed to slightly influence partner choice decisions in men: they were more likely to indicate their willingness to go another date if they rated their female partner's voice as attractive. However, the effect was small, especially when compared to the effect that visual attractiveness had on male partner choice decisions. For women, no clear effect of auditory attractiveness on their partner choice decisions was observed in the partial model, although the independent model showed a similar pattern for both men and women. These findings are somewhat consistent with previous research (Asendorpf et al., 2011), that found a smaller effect of vocal attractiveness than visual attractiveness, although the effect of vocal attractiveness was significant. It is important to note, though, that Asendorpf et al. (2011) obtained visual and auditory attractiveness ratings from an independent group of raters, while we used individual attractiveness ratings to predict dating outcome. Therefore, it is not clear whether these findings are directly comparable. However, the fact that a study using independent raters finds a similar strong effect of visual attractiveness on date outcome shows how important facial attractiveness is, and at the same time suggests it is unlikely that potential demand characteristics underlie our main result.

Furthermore, the effect of auditory attractiveness on dating outcomes might be obfuscated by voice modulation and interpersonal dynamics during speed-dates. People modulate the pitch of their voice when addressing a desirable partner (Fraccaro et al., 2011; Leongómez et al., 2014; Pisanski et al., 2018). In addition, the presence and sound of other people, and a camera recording the interaction, might have further affected the mental states of the participants and, consequently, their voices. Therefore, it is likely that participant's spoke differently (e.g., different pitch) during the audio recordings and the actual dates, leading to the discrepancies in perception of the recorded voice and the voice that was heard on the date on the rater's end. Thus, using an isolated rating task for voices might have slightly obscured the importance of voice during the actual dates. Future research should compare how isolated measures of vocal attractiveness relate to vocal attractiveness in an explicitly social context such as a date.

We found a small effect of olfactory attractiveness on willingness to date again for women, but not for men. Interestingly, the relationship that we found for women was negative: they were less likely to want to go on another date with men whose smell they rated as attractive. This direction of the effect is surprising given previous evidence suggesting that scent plays an important role in mate selection for women (Havlíček et al., 2008). It is unclear why this effect might have occurred. One possible explanation is a methodological one: the olfactory samples employed in the present study should be perceived as indicators of diplomatic body odour (Gaby & Zayas, 2017). Diplomatic body odour samples might be more ecologically valid than natural body odour samples, as odours are heavily affected by the use of hygiene products and personal habits in real life, which may interfere with olfactory cues for mate choice (Allen et al., 2016; Gaby & Zayas, 2017; Sorokowska et al., 2016). With regard to the negative correlation we found, it can theoretically be possible that men who know they have a strong body odour used extra hygiene products when wearing the t-shirt, even though they were instructed not to. This would then result in high attractiveness ratings for odour, while the actual smell perceived on the date would be unpleasant. Note that this explanation does assume that women actually perceived the natural odour during the date. Because we have no compliance data for the t-shirt preparation, we can unfortunately not exclude this explanation. Such potential dicrepancies between different types of body odour highlight the difficulties of studying the effects of olfaction on human mate choice (Ferdenzi et al., 2020), and future studies could consider incorporating both natural and diplomatic samples.

Importantly, some important questions about multimodal attractiveness and initial attraction remain. For example, a question that we have not investigated is how cross-modal interactions shape attraction. Given our sample is relatively small, we could not examine such complex relationships. Nonetheless, investigating such dynamics might be vital to grasp the complex dynamics of multimodal attractiveness (Groyecka et al., 2017). For example, having an attractive voice and an attractive face might especially increase dating success, or unattractiveness on one modality might reduce the positive effect of the other modality (Demattè et al., 2007). We suggest that large-scale studies using a similar design to our studies are necessary to further elucidate these complex interactions. Another example concerns the context-dependent importance of the different modalities. Visual and vocal attractiveness might be especially important during first interactions in which close contact is rare. Olfactory attractiveness, however, may be important during more advanced stages of the relationship (Groyecka et al., 2017), when close contact is more common, or during first interactions with close physical contact. Altogether, investigating cross-modality interactions and context-dependence are essential to understand how multimodal attractiveness shapes initial attraction.

In conclusion, our results corroborate the importance of visual attractiveness in early stages of mate choice. At the same time, the static attractiveness ratings for auditory and olfactory attractiveness did not substantially predict date outcome. This suggests that especially visual attractiveness is relatively important during speed-dates, while auditory and olfactory attractiveness are less important. Nonetheless, these modalities might come into play in other stages of the developing relationship or in other contexts. Furthermore, attractiveness of voice and smell may be more strongly influenced by dynamics during an interaction, rendering static attractiveness ratings to be less predictive. Altogether, our findings illustrate that the coupling of multimodal rating tasks and speed-date paradigms is a fruitful method of studying multimodal human mate choice. Applying such methods with large-scale samples allows for disentangling the effects of different factors on date outcome, and could further aid in understanding how human mate choice is affected by sight, sound, and scent.

Chapter 4

Attractiveness modulates attention, but does not enhance gaze cueing

Abstract

Attractiveness is an important aspect of human society. Attractive people enjoy multiple societal privileges and are assigned positive personality traits, and both men and women find attractiveness important when it comes to partner choice. Our universal preference for beauty might be reflected in implicit perception of human faces. In a series of three studies, we use Bayesian methods to investigate whether attractiveness or attractive traits modulate implicit attention and gaze cuing in a large community sample. In Experiment 1, we used a dot-probe task to measure attentional bias toward attractive faces. The results demonstrate that participants reacted faster when the probe appeared behind an attractive face but not when it appeared behind an unattractive face, suggesting that specifically attractive faces captured attention. In Experiment 2, we used a similar method to test whether facial symmetry, an often-mentioned characteristic of attractive faces, modulated attention. However, we found no such effect. In Experiment 3, we used a gaze-cuing task to test whether participants were more likely to follow the gaze of attractive faces, but no such effect was found. To conclude, attractiveness affects our implicit attention toward faces, but this does not seem to extend to gaze cuing.

Based on:

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/MLGUDE

Introduction

Beauty is an important aspect of our social environment, as reflected in the high prevalence of attractive people featured on billboards, in magazines, and on TV. The use of expressive and almost perfectly symmetrical faces is meant to attract our attention. This choice is reasonable, given that the preference for attractive faces is widespread, expressed in some aspects of daily life (Langlois et al., 2000) and already present in newborn infants (Damon, Mottier, et al., 2017). Relatively speaking, attractive people enjoy more societal privileges (Little, Jones, et al., 2011), are assigned positive personality traits (Dion et al., 1972; Griffin & Langlois, 2006), and can choose from a greater pool of potential mates (Karraker et al., 2017). In addition, attractiveness might be positively associated with health (Nedelec & Beaver, 2014; Shackelford & Larsen, 1999; but see Cai et al., 2019). Thus, attractiveness serves as an important cue that can bias social decision making. In the current article, we investigate whether attractive and symmetrical faces modulate attention more readily than unattractive and asymmetrical faces, as well as whether attractive faces enhance gaze cuing more strongly than unattractive faces.

Facial attractiveness is especially important in partner choice (Rhodes, 2006; Thornhill & Gangestad, 1999), and this is evident from the fact that attractive faces capture and hold our attention (Lindell & Lindell, 2014). Being able to readily detect an attractive potential mate and interpret their emotions, intentions, and focus of attention might convey evolutionary benefits. Namely, it allows for the selection of suitable partners from the environment (Maner & Ackerman, 2015) and consequently bond with them (Müller et al., 2013). Whether attractive faces attract attention for these reasons or, alternatively, because they stand out and are oddballs in the environment is unclear from previous studies (Ma et al., 2019; Ma, Zhao, et al., 2015). These studies have established that attention is modulated by attractive faces relative to intermediately attractive faces. However, it is possible that unattractive faces might modulate attention in a similar fashion. Therefore, it is necessary to incorporate both attractive and unattractive faces to elucidate how this attentional bias might arise. Moreover, the topic of how attractiveness mediates perception of variant facial cues, such as gaze, has received relatively little attention, even though this has been investigated for other more subtle facial characteristics, such as familiarity (Deaner et al., 2007) and dominance (Jones et al., 2010; Ohlsen et al., 2013).

Given our strong preference for attractive individuals, it is not surprising that beauty modulates attention. Indeed, humans automatically attend to attractive faces of opposite-sex individuals (Lindell & Lindell, 2014). Previous research has shown that this attentional bias is evident in both sustained and implicit attention paradigms. For example, in free-viewing paradigms where two faces are presented at the same time, people attend longer to the more attractive face (Leder et al., 2016). Crucially, sustained attention for attractive faces is still apparent after controlling for low-level features, such as luminance and contrast (Li et al., 2016), suggesting that the actual configuration of the face contributed to the attentional bias and not just low-level differences between attractive and unattractive faces. Furthermore, it has recently been suggested that attractiveness interferes with top-down goals. Specifically, presenting attractive faces reduces performance in a visual search task and target orientation judgment (Nakamura & Kawabata, 2014; Sui & Liu, 2009).

A well-known paradigm by which attentional biases can be measured is the dot-probe task (MacLeod et al., 1986; van Rooijen et al., 2017). In the dot-probe task, participants view two photographic stimuli presented briefly (typically for approx. 300 ms) on the left and right of the display. Next, one of these stimuli is replaced by a probe. Participants are instructed to quickly and accurately indicate the location of the probe. The interpretation of possible results is straightforward: Since participants selectively attend to salient images, participants respond faster when the probe appears at the same location as the attention-grabbing image (i.e., a congruent trial). Thus, we can infer attentional biases from reaction times (RTs) in the dot-probe task. This paradigm has also been used to investigate attentional bias as a function of attractiveness. For example, Maner et al. (2007) used a modified dot-probe paradigm that presented only one picture per trial. Their findings showed that participants disengaged slower from attractive faces than neutral faces, suggesting that attractiveness holds attention. This effect has since been replicated in further studies that employed the original dot-probe paradigm (Ma et al., 2019; Ma, Zhao, et al., 2015): They found that single individuals had trouble disengaging from attractive faces but did not find evidence that attractive faces capture attention. Thus, while both studies found evidence for a disengagement effect of attractiveness, evidence for immediate capture of attention has not been found using the dot-probe paradigm.

However, the previous studies investigating bottom-up effects of attractiveness on attention suffer from three methodological limitations. First, Ma et al. (2015, 2019) paired face stimuli with pictures of objects. Therefore, instead of two faces competing for attention (e.g., attractive and intermediately attractive), there was one face and one household object. Thus, the saliency of the neutral stimuli differed very strongly from the faces they were paired with. Second, Ma and colleagues and Maner et al. (2007) only compared attractive faces with intermediately attractive faces. Given that both attractive and unattractive faces may possess features that distinguish them from an average face (Lin et al., 2020; Said & Todorov, 2011), including the comparison between intermediately attractive and unattractive faces is necessary to conclude that specifically attractive faces modulate attention. Third, Ma and colleagues presented stimuli for 500 ms, which is not an ideal presentation duration to study initial engagement, because individuals can shift attention within this time period (Petrova et al., 2013). As a consequence, it remains unclear whether the attractiveness of a face influences immediate attentional capture.

Apart from a general preference for attractiveness, humans also have an aesthetic preference for symmetry (Bertamini et al., 2019; Che et al., 2018; Little, 2014). Importantly, this preference seems widespread in nature: Bilateral symmetry is associated with increased mating success in multiple animal species (Møller & Thornhill, 1998). In humans, attractive faces tend to be more symmetrical than unattractive faces (Perrett et al., 1999; Rhodes et al., 1999). People perceive them as healthy looking (Jones et al., 2001; Rhodes et al., 2007), and indeed, symmetry has been linked to genetic health and developmental stability, which would explain why a preference for symmetrical partners could be beneficial (Little, Jones, et al., 2011). Because of the saliency of symmetry, Wagemans (1995) suggested that it should be detected rapidly. While it has been shown that women can correctly identify symmetrized versions of a male face in a forced-choice paradigm (Oinonen & Mazmanian, 2007), it has not yet been established whether such symmetrical faces rapidly modulate the attention of viewers. The evolutionary significance of symmetry might translate into an attentional bias toward symmetrical partners. Thus far, no study has directly investigated whether that is indeed the case by comparing modulation of attention by symmetrized, original, and asymmetrized stimuli.

Because humans have such a strong preference for attractive people, they might pick up other variant and invariant facial characteristics more readily in attractive faces. For example, people identify facial expressions more quickly in attractive faces than in unattractive faces (Taylor & Bryant, 2016) and classify attractive faces more rapidly and accurately in a sex classification task (Hoss et al., 2005). In addition, one may want to know what information an attractive person is perceiving from the environment by following their gaze to infer their desires and goals (Baron-Cohen, 2014) and obtain social information about them. These sources of information might increase the likelihood of a successful approach, because the network of collected information can help to create an exchange of shared interests. Alternatively, mimicking the gaze of attractive opposite-sex conspecifics might facilitate becoming the object of attraction, because mimicking can increase bonding (Chartrand & Lakin, 2013; Prochazkova & Kret, 2017). In line with this idea, single people are more likely to mimic attractive others (Birnbaum et al., 2019; Farley, 2014), and couples show more mimicry compared to platonic friends (Maister & Tsakiris, 2016). Thus, copying the gaze direction of an attractive other might enhance bonding. However, it has not been established whether this translates to mimicking the gaze direction of attractive faces. Previous studies have reported that familiarity (Deaner et al., 2007) and facial masculinity (Jones et al., 2010; Ohlsen et al., 2013) enhance gaze cuing. It is not known, however, whether people are following the gaze direction of an attractive other more readily than that of an unattractive other. These previously observed effects of familiarity and facial masculinity might generalize to facial attractiveness of both males and females as well.

Age and sex of the perceivers might modulate biases toward attractiveness. Previous studies on age and attractiveness perception have found that older people are less selective when it comes to rating faces on attractiveness: Overall, they give higher attractiveness ratings than younger people (Ebner et al., 2018; Kiiski et al., 2016). This bias also translates to memory: Younger people show better memory for attractive faces than older people (Lin et al., 2020). These results are in line with the idea that attractiveness is of reduced relevance for older people. In contrast, for younger people, it might be a salient social signal that they, for example, use to identify suitable mates. Similarly, attractiveness might be a more salient signal for men than for women. This is reflected in the fact that men report that they find attractiveness more important when it comes to mate choice than women (Bech-Sørensen & Pollet, 2016; Sprecher et al., 1994) and that men will exert more effort to see attractive opposite-sex faces than women (Hayden et al., 2007). Thus, the bias for attractive faces may differ between age groups and sexes.

In the present study, we investigated attractiveness biases in a large Western community sample of adults with a wide age range. We examined (a) whether people have an attentional bias toward attractive faces and unattractive faces, compared to intermediately attractive faces in a dot-probe task; (b) whether subtle differences in facial symmetry, a trait that has been linked to attractiveness, modulate attention in a dot-probe task; and (3) whether facial attractiveness modulates gaze following a modified Posner cuing task. Unattractive and asymmetrical faces were added as a control as they form another "extreme" category of a face type that is, like very attractive or symmetrical faces, not very common.

In Experiment 1, if participants would selectively attend to more attractive faces, we expected faster RTs on trials in which the probe appeared behind the attractive face (in the attractive vs. intermediate condition) and possibly the intermediate face (in the unattractive vs. intermediate condition). However, if participants would selectively attend to both attractive and unattractive faces because both deviate from the average face, we expected faster RTs on trials in which the probe appeared behind the attractive face (in the attractive vs. intermediate condition) and unattractive face (in the unattractive vs. intermediate condition). We had similar expectations for Experiment 2; if facial symmetry is a salient social signal, we would expect participants to selectively attend to the most symmetrical face in each condition. However, if very symmetrical and asymmetrical faces both attract attention because they deviate from average, we would expect faster RTs on trials where the probe appears behind the symmetrized or asymmetrized stimulus (paired with original picture). Furthermore, in Experiment 3, we expected that people would follow the gaze direction of attractive faces particularly, which would make them respond faster on congruent trials where the probe appeared in the location the attractive face was gazing at. In addition, in all three experiments, we expected the biases to be more pronounced in male participants and in younger participants, since attractiveness is a more salient signal for these groups.

Experiment 1

Method

Participants

Experiment 1 included 150 participants (82 females, mean age = 31.49 years, *SD* = 12.79, ranging from 18 to 74 years old). Participants were visitors at the Apenheul Primate Park (Apeldoorn, the Netherlands). All participants self-reported normal or corrected-to-normal vision and were heterosexual. The experimental procedures were in accordance with the Declaration of Helsinki, and the study was reviewed and approved by the Psychology Ethics Committee of Leiden University (CEP17-0719/254). Participants were not compensated for their participation.

Experimental Design

The experiment held a randomized within-subjects design, where independent variables comprised attractiveness category of the stimuli, participant's age, and sex. The dependent variable was RT (in ms).

Apparatus

The task was performed on a touchscreen (Dell corporation, model S2240Tb, 21.5 in., 1,920 × 1,080 pixels), which was connected to a Dell laptop computer (model OPTIPLEX 990) and ran via E-Prime (Version 2.0; Psychology Software Tools). The touchscreen was located in a public but quiet corner of an indoor visitor enclosure of the park. To minimize potential distractors, we set up the touchscreen on a table adjacent to a wall. Participants sat at a distance of approximately 60 cm from the touchscreen.

Stimuli

Stimuli were selected from the Chicago Face Database (CFD) 2.3 (Ma, Correll, et al., 2015). This face database consists of 597 high-resolution, standardized color photographs of male and female faces of varying ethnicity between the ages of 18 and 65 years. The faces have been validated previously by independent judges on several scales, including on attractiveness (Ma, Correll, et al., 2015). Based on these CFD attractiveness ratings, we selected stimuli depicting 10 attractive, 10 unattractive, and 20 intermediately attractive White individuals.

We tested whether age differed between the stimulus categories, using a Bayesian two-way analysis of variance (Sex × Attractiveness Category), since older faces may be perceived as less attractive than younger faces (Ebner, 2008). We found moderate evidence for the null hypothesis that age did not differ between the sexes (BF_{01} = 4.18 ± .02%) and attractiveness categories (BF_{01} = 3.72 ± .03%). In addition, we found strong evidence for the null hypothesis when testing the interaction between sex and attractiveness category (BF_{01} = 78.95 ± .67%), suggesting that age did not substantially differ across stimulus categories.

Procedure

The experiment involved a dot-probe paradigm (MacLeod et al., 1986; for a review, see van Rooijen et al., 2017). In the task, two stimuli were presented next to each other, each centralized in one half of the screen. All paired images consisted of an attractive or unattractive face and an intermediately attractive face. Location of the stimuli and the probe was balanced between trials. Participants only saw pictures of opposite-sex individuals. In total, participants performed 80 trials presented in random order (excluding five practice trials).[1]

The sole instruction participants received was to tap on a black dot as fast as they could (Figure 1). Every trial started with a dot appearing in the midbottom of the screen until participant response. Subsequently, two stimuli (i.e., an (un) attractive and an intermediately attractive face) were displayed for 300 ms. Next, a dot (probe) appeared in place of either the (un)attractive face or in place of the intermediately attractive face. The probe remained on the screen until participant response. Every trial ended with a 2,000-ms intertrial interval. The RT of the participant from tapping on the probe from stimulus offset was used as a dependent variable in all further analyses.

After the experiment, participants validated all 40 stimuli (presented in a random order) by rating their attractiveness on a 7-point ordinal scale (*very unattractive, fairly unattractive, somewhat unattractive, neutral, somewhat attractive, fairly unattractive, very unattractive*). We used these scores to determine whether the ratings of the participants aligned well with the predetermined attractiveness categories (attractive, intermediate, unattractive).

Statistical Analyses

We first filtered out extremely fast or slow responses. For fast trials, we excluded all trials with RTs < 250 ms. The upper exclusion level was determined per subject. Specifically, we computed the median RT and the median absolute deviation (Leys et al., 2013) per subject. The following conservative filter was applied per subject (upper limit RT = median + 2 * median absolute deviation). The lower and upper filter resulted in exclusion of 4.7% overall. Hereafter, we mean-centered the RTs by subject (i.e., how fast did the participant react relative to their own mean RT).

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[1] Due to a coding error, an additional sensitive, touchable area was presented in the middle of the screen on the slide showing the probe. Technically, a participant's RT could be logged if they clicked this additional sensitive area instead of the probe. However, because this sensitive area was transparent and thus invisible to the participants, it is highly unlikely that they tapped within that area instead of tapping the probe. Also, the fact that no participants had an extreme amount of extremely fast or extremely slow responses suggests that they were following the instruction to tap the probe properly.

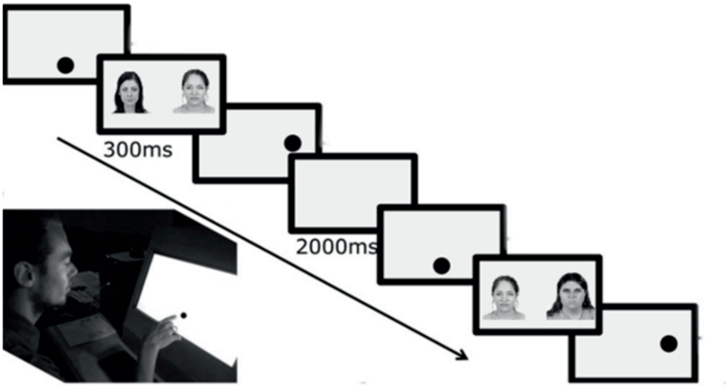

Figure 1. Trial Outline of the Dot-Probe Task. Stimuli from Chicago Face Database (https://chicagofaces.org/default/). Copyright 2015 by University of Chicago, Center for Decision Research. Adapted with permission.

All analyses were done in R statistics Version 4.2 (R Core Team, 2018). We fitted Bayesian mixed models using the brms package (Bürkner, 2017, 2018). Bayesian analyses have gained in popularity over the past few years because they have a number of benefits compared to frequentist analyses (Kruschke et al., 2012; Makowski et al., 2019). While frequentist methods (e.g., *p*-value null-hypothesis testing; see Wagenmakers, 2007) inform us about the credibility of the data given a hypothesis, Bayesian methods inform us about the credibility of our parameter values given the data that we observed. This is reflected in the different interpretation of frequentist and Bayesian confidence intervals: The first is a range of values that contains the estimate in the long run, while the latter tells which parameter values are most credible based on the data (Kruschke et al., 2012; McElreath, 2018). Furthermore, Bayesian methods allow for the inclusion of prior expectations in the model, are less prone to Type I errors, and are more robust in small and noisy samples (Makowski et al., 2019). Altogether, these reasons make Bayesian methods a useful tool for data analysis.

First, we investigated whether the attractiveness ratings of the stimuli given by our subjects matched with the categories that we used. To examine this question, we fitted a Bayesian mixed model with an ordinal dependent variable (attractiveness rating, seven levels) and the interaction between sex and attractiveness category as independent variables. Furthermore, we added random intercepts per subject and stimulus and allowed the effect of attractiveness category to vary by subject by adding random slopes. We used regularizing Gaussian priors with $M = 0$ and

SD = 1 for the fixed effects, default Student *t* priors with 3 degrees of freedom for the thresholds, and default half Student *t* priors with 3 degrees of freedom for the random effects and residual standard deviation.

To test our main hypothesis, we created a model that used by-subject mean-centered RT as the dependent variable and the interaction between condition (attractive vs. intermediate or unattractive vs. intermediate) and probe location (behind intermediate or behind (un)attractive stimulus). Furthermore, to explore the effect of sex and age, we created two more complex models that included the three-way interaction between condition, probe location, and sex and age, respectively. All categorical fixed effects were sum-to-zero coded, and age was *z*-transformed. In all models, we added random intercepts per subject and trial number (to control for order effects) and allowed slopes of the interaction between condition and probe location to vary by subject. We used regularizing Gaussian priors with *M* = 0 and *SD* = 5 for all fixed effects, a Gaussian prior with *M* = 0 and *SD* = 10 for the intercept, and default half Student *t* priors with 3 degrees of freedom for the random effects and residual standard deviation, which were weakly informative.

We used multiple measures to summarize the posterior distributions for each variable: (a) the median estimate and the median absolute deviation of this estimate, (b) the 89% credible interval (CI; McElreath, 2018), and (c) the probability of direction (*pd*). The 89% CI indicates the range within which the effect falls with 89% probability, while the *pd* indicates the proportion of the posterior distribution that is of the median's sign (Makowski et al., 2019). We have chosen an 89% CI instead of the conventional 95% to reduce the likelihood that the CIs are interpreted as strict hypothesis tests (McElreath, 2018). Instead, the main goal of the credible intervals is to communicate the shape of the posterior distribution.

Furthermore, we used leave-one-out cross-validation (PSIS-LOO-CV; Vehtari et al., 2017) to compare the predictive accuracy of the more complex models that include sex and age, respectively, to that of the simpler model. Using PSIS-LOO-CV, we calculated the expected log predictive density (elpdLOO), which quantifies predictive accuracy, for each model. Then, we calculated the difference in elpdLOO (ΔelpdLOO) between the models and the standard error of the difference. If ΔelpdLOO is small (< 4) and the *SE* is large relative to the difference, this suggests that models have similar predictive performance.

All models were run with four chains of 3,000 iterations (500 warmups), resulting in a total posterior sample of 10,000. Furthermore, we checked whether the models converged by inspecting trace plots and histograms, as well as checking the Gelman–Rubin diagnostic (Depaoli & van de Schoot, 2017). For all models, no indication of divergence was found.

Results

Validation of stimuli

The ordinal mixed model showed that subjects gave substantially higher attractiveness ratings to stimuli that were classified as attractive and lower ratings to stimuli that were classified as unattractive (Figure 2). This was the case for both women ($\Delta \text{estimate}_{\text{attractive-intermediate}}$ = 2.11 [.30], 89% CI [1.63, 2.61], pd = 1.00; $\Delta \text{estimate}_{\text{unattractive-intermediate}}$ = −1.45 [.31], 89% CI [−1.94, −.96], pd = 1.00) and men ($\Delta \text{estimate}_{\text{attractive-intermediate}}$ = 3.17 [.59], 89% CI [2.22, 4.11], pd = 1.00; $\Delta \text{estimate}_{\text{unattractive-intermediate}}$ = −1.73 [.32], 89% CI [−2.25, −1.22], pd = 1.00).

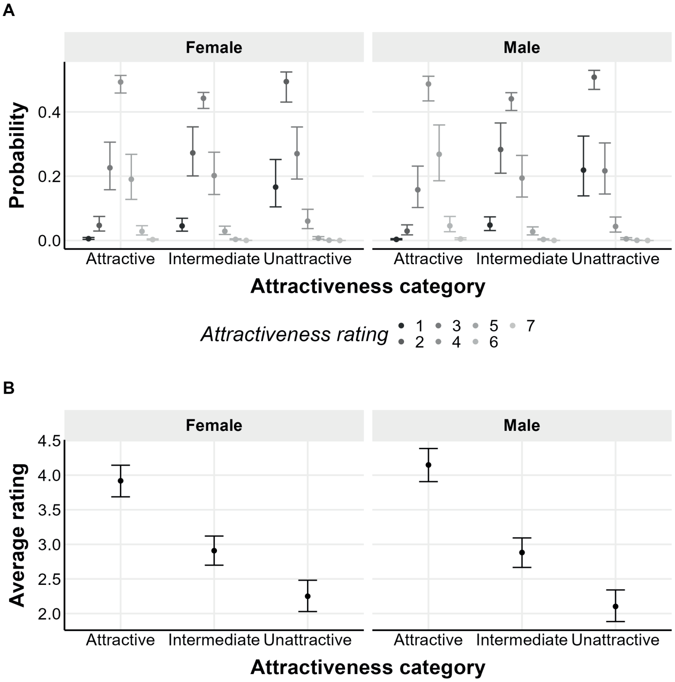

Figure 2. Validation of the Stimuli of Experiment 1. Probability of receiving high attractiveness ratings was higher for stimuli categorized as "attractive" (a). This is also depicted in (b), which treats the ratings as a continuous variable for visualization purposes. See the online article for the color version of this figure.

Simple Model

To test our main prediction that attractiveness would significantly influence RT, we ran a Bayesian mixed model with by-subject mean-centered RT per trial as the dependent variable and the interaction between condition and probe location as independent variables (Table 1; see Appendix G for model stability checks). We found a robust interaction effect of condition and probe location (Figure 3), meaning that people reacted faster on trials in which the probe appeared behind an attractive face than when it appeared behind an intermediate (median difference = 9.23 [2.21], 89% CI [5.67, 12.74], *pd* = 1.00), while an opposite pattern was found when unattractive faces were paired with intermediate faces (median difference = −6.92 [2.33], 89% CI [−3.29, −10.56], *pd* = .99).

Table 1. Model Output for the Simple Model of Experiment 1. Note: all categorical independent variables were sum-to-zero coded.

Parameter	Median estimate	SD	89% CI lower bound	89% CI upper bound
Intercept	0.17	1.54	-2.26	2.73
Probe Location [intermediately attractive]	0.58	0.69	-0.52	1.69
Condition [attractive vs. intermediate]	-1.88	0.71	-3.02	-0.75
Condition [attractive vs. intermediate]: Probe Location [intermediately attractive]	4.03	0.88	2.64	5.45
Random effects				
sd [intercept] Trial order	12.36	1.27	10.50	14.54
sd [intercept] Subject	0.47	0.42	0.05	1.34
sd [by-subject slope] Probe Location [intermediately attractive]	0.96	0.82	0.10	2.62
sd [by-subject slope] Condition [attractive vs. intermediate]	1.81	1.05	0.26	3.59
sd [by-subject slope] Condition [attractive vs. intermediate]: Probe Location [intermediately attractive]	6.58	1.04	4.94	8.25
N_{obs} = 11437				
N_{subj} = 150				

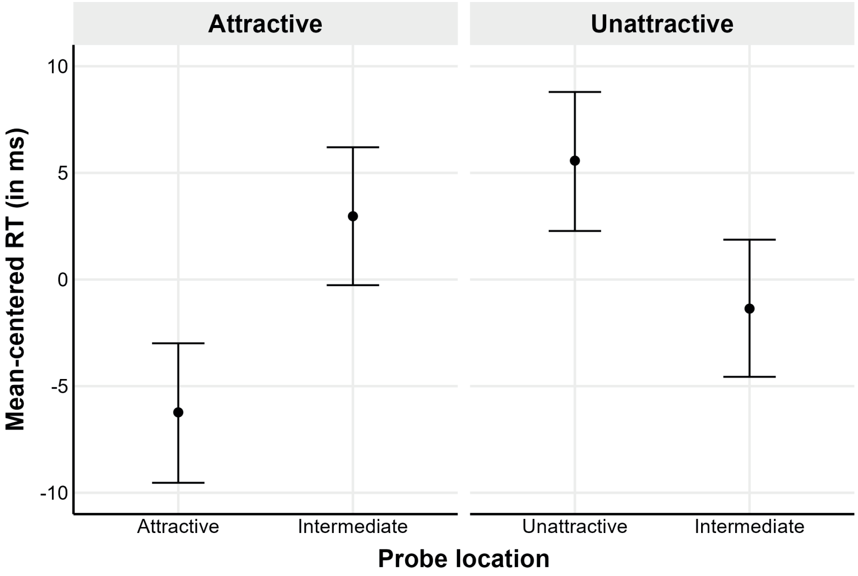

Figure 3. By-Subject Mean-Centered RTs per Condition and Probe Location. Dots indicate the median reaction time (RT), while error bars represent the 89% credible interval. In the attractive conditions, participants reacted faster when the probe appeared behind the attractive face. The opposite pattern was found for unattractive faces. This suggests that specifically attractive faces modulate initial attention.

Age and Sex

We investigated whether adding either age or sex to the model did improve the predictive accuracy relative to the simple model. When comparing the model that included the three-way interaction between age, condition, and probe location to the simple model, we found that the predictive accuracy of the simple model was slightly better ($\Delta\text{elpd}_{\text{LOO}}$ = 3.5 [.9]). For the model that included the three-way interaction between sex, condition, and probe location, on the other hand, we found that it performed slightly better than the simple model. However, the difference was small and the standard error of the difference was relatively large ($\Delta\text{elpd}_{\text{LOO}}$ = 3.7 [3.6]). Altogether, this suggests that adding age or sex to the simple model did not substantially increase the predictive accuracy.

Experiment 2

Method

Participants

Experiment 2 included 150 new participants. Participants had normal or corrected-to-normal vision and could participate regardless of their sexual orientation. However, given the small number of nonheterosexual participants (*N* = 10), they were excluded from further analyses. Therefore, the data set for Experiment 2 included 140 participants (68 females, mean age = 38.66 years, *SD* = 11.64, ranging from 17 to 67 years old). Participants were visitors at the Apenheul Primate Park (Apeldoorn, the Netherlands). The experimental procedures were in accordance with the Declaration of Helsinki, and the study was reviewed and approved by the Psychology Ethics Committee of Leiden University (CEP19-0612/343). Participants were not compensated for their participation.

Experimental Design

The experiment held a randomized within-subjects design, where the fixed factor comprised the location of the probe (behind symmetrical or asymmetrical face) and the combination (symmetrized vs. original, asymmetrized vs. original, symmetrized vs. asymmetrized). The dependent variable was RT (in ms).

Apparatus

The task was performed on a touchscreen (Iiyama ProLite T1930SR-1, 1,280 × 1,024 pixels), which was connected to a Dell desktop computer (model OPTIPLEX 3020) and ran via E-prime (Version 2.0; Psychology Software Tools). The touchscreen was located in a public but quiet corner of the park. To minimize potential distractors, we set up the touchscreen on a table adjacent to a wall. Participants sat at a distance of approximately 60 cm from the touchscreen.

Stimuli

We selected faces from the Young Adult White Faces Dataset (DeBruine & Jones, 2017). This stimulus set contains manipulated and original portraits of 20 young men and 20 young women with a neutral facial expression. We used the 50% symmetric, 50% asymmetric, and the original portraits of each individual. This allowed us to test whether subtle differences in facial characteristics of the same individual modulated attention.

Procedure

The experiment involved a dot-probe paradigm, similar to Experiment 1. Participants performed 60 trials, consisting of 20 trials of three different combinations (i.e., symmetrical-original, asymmetrical-original, symmetrical-asymmetrical). Within each combination, the probe appeared 10 times behind each category, and the location of the probe was balanced. Participants were only presented with pictures of opposite-sex individuals. The participants' RT to the probe was the dependent variable for our analyses.

Statistical Analyses

We first excluded extremely fast and slow reactions times, following the same method as described for Experiment 1. The lower and upper filter resulted in exclusion of 524 of 9,000 trials (6.24%). We further excluded two subjects because the filtering criterion resulted in more than 25% of their responses being excluded. Therefore, the final data set contained 7,789 trials of 138 participants (67 females).

Our statistical methods were similar to those described for Experiment 1, with a few exceptions. To test our hypothesis, we created a model that used by-subject mean-centered RT as the dependent variable and the interaction between condition (symmetrized vs. original, asymmetrized vs. original, symmetrized vs. asymmetrized) and probe location (behind symmetrical/behind asymmetrical face). Furthermore, in contrast to Experiments 1 and 3, this experiment did not include a stimulus validation.

Results

Simple Model

To test our main prediction that facial symmetry would significantly influence RT, we ran a Bayesian mixed model with by-subject mean-centered RT per trial as the dependent variable and the interaction between condition and Probe Location as independent variables (Table 2; see Appendix G for model stability checks). We found no effect of facial symmetry on RT in any of the three conditions (Figure 4); in each condition, the differences in RT between the probe locations were negligible (asymmetrized vs. original: median difference = −1.01 [3.05], 89% CI [−5.92, 3.82], *pd* = .63; symmetrized vs. original: median difference = .99 [2.91], 89% CI [−3.69, 5.66], *pd* = .64; symmetrized vs. asymmetrized: median difference = 1.67 [2.97], 89% CI [−3.14, 6.32], *pd* = .71).

Table 2. Model Output for the Simple Model of Experiment 2. Note: all categorical independent variables were sum-to-zero coded.

Parameter	Median estimate	SD	89% CI lower bound	89% CI upper bound
Intercept	0.44	2.15	-2.98	3.93
Condition [asymmetrized-original]	0.76	1.20	-1.19	2.67
Condition [symmetrized-original]	-1.67	1.21	-3.62	0.23
Probe Location [most symmetrical]	0.28	0.87	-1.10	1.66
Condition [asymmetrized-original]:Probe Location [most symmetrical]	-0.79	1.21	-2.70	1.17
Condition [symmetrized-original]:Probe Location [most symmetrical]	0.25	1.19	-1.65	2.14
Random effects				
sd [intercept] Trial order	15.51	1.78	12.99	18.63
sd [intercept] Subject	0.59	0.53	0.06	1.67
sd [by-subject slope] Condition [asymmetrized-original]	2.34	1.74	0.22	5.60
sd [by-subject slope] Condition [symmetrized-original]	1.98	1.58	0.21	5.16
sd [by-subject slope] Probe Location [most symmetrical]	1.68	1.28	0.18	4.17
sd [by-subject slope] Condition [asymmetrized-original]:Probe Location [most symmetrical]	2.26	1.75	0.23	5.69
sd [by-subject slope] Condition [symmetrized-original]:Probe Location [most symmetrical]	2.69	1.88	0.27	6.12
$N_{obs} = 7789$				
$N_{subj} = 138$				

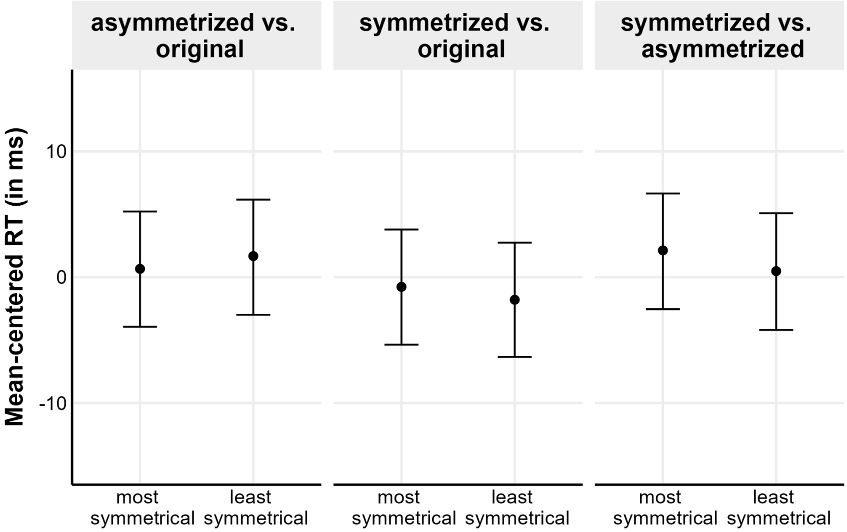

Figure 4. By-Subject Mean-Centered RTs per Condition and per Probe Location. Dots indicate the median reaction time (RT), while error bars represent the 89% credible interval. As can be seen, symmetry did not substantially affect reaction time in any of the three conditions.

Age and Sex

We investigated whether adding either age or sex to the model did improve the predictive accuracy relative to the simple model. Both the model including sex (Δelpd_{LOO} = 4.4 [1.7]) and the model including age (Δelpd_{LOO} = .5 [2.9]) had a slightly lower predictive accuracy than the simple model. Altogether, this suggests that including age or sex did not improve the predictive accuracy of the model.

Experiment 3

Method

Participants

Experiment 3 included 150 new participants (73 females, mean age = 30.98 years, *SD* = 12.65, ranging from 18 to 70 years old). Participants were visitors at the Apenheul Primate Park (Apeldoorn, the Netherlands). All participants self-reported normal or corrected-to-normal vision and were heterosexual. The experimental procedures were in accordance with the Declaration of Helsinki, and the study was reviewed and approved by the Psychology Ethics Committee of Leiden University (CEP18-0531/272). Participants were not compensated for their participation.

Experimental Design

The experiment held a randomized within-subjects design, where independent variables comprised congruence (looking direction congruent with dot or not), attractiveness category of the stimulus (attractive, intermediate, unattractive), age, and sex. The dependent variable was RT (ms).

Stimuli

Faces were selected from the Oslo Face Database (Chelnokova et al., 2014). This database includes 200 faces (100 females) with a neutral expression and with three gaze directions: left, center, and right. All stimuli have been rated for attractiveness. Based on these ratings, we chose 10 attractive, 10 intermediate, and 10 unattractive faces of each sex.

The ages of the people in the photographs were not recorded, so it was not possible to analyze whether age differed between the stimulus categories. However, because the database consists of pictures of students, it is likely that they are in the same age range.

Procedure

The procedure and apparatus for Experiment 3 were similar to Experiment 1. However, we used a modified Posner cuing task (Deaner et al., 2007; Posner, 1980) to test gaze following. Instead of showing two pictures on the side, one front-facing picture was presented in the middle of the screen for 300 ms. Hereafter, the same face was again presented in the middle of the screen but now looking either to the left side or the right side of the screen for 300 ms. After this, the location of the probe would either be congruent (same side as looking direction) or incongruent (opposite side of looking direction (Figure 5). Participants performed 60 trials in total.[2]

As in Experiment 1, participants validated all stimuli (both front-facing and side-facing) after the experiment in a randomized order by rating their attractiveness on a 7-point ordinal scale. Again, we used these scores to determine whether the ratings of the participants aligned well with the predetermined attractiveness categories (attractive, intermediate, unattractive). Subjects rated both the central-looking stimuli and the side-looking stimuli. However, because central and side ratings correlated very strongly ($r_s = .82$, 89% CI [.82, .83], *pd* = 1.00), we used only the central ratings for further validation.

Statistical Analyses

We first excluded extremely fast and slow reactions times, following the same method as described for Experiment 1. The lower and upper filter resulted in exclusion of 476 of 9,000 trials (5.29%). The highest number of excluded trials per participant was 10.

Our statistical methods were similar to those described for Experiment 1, with a few exceptions. To test our hypothesis, we created a model that used by-subject mean-centered RT as the dependent variable and the interaction between attractiveness category (attractive, intermediate, unattractive stimulus) and gaze congruency (probe location congruent/incongruent with gaze direction). Due to convergence problems, it was not possible to add by-subject random slopes for the interaction to the model; therefore, the random-effect structure consisted of only random intercepts per subject and trial number.

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[2] Due to a coding error, an additional sensitive, touchable area was presented in the middle of the screen on the slide showing the probe. Technically, a participant's RT could be logged if they clicked this additional sensitive area instead of the probe. However, because this sensitive area was transparent and thus invisible to the participants, it is highly unlikely that they tapped within that area instead of tapping the probe. Also, the fact that no participants had an extreme amount of extremely fast or extremely slow responses suggests that they were following the instruction to tap the probe properly.

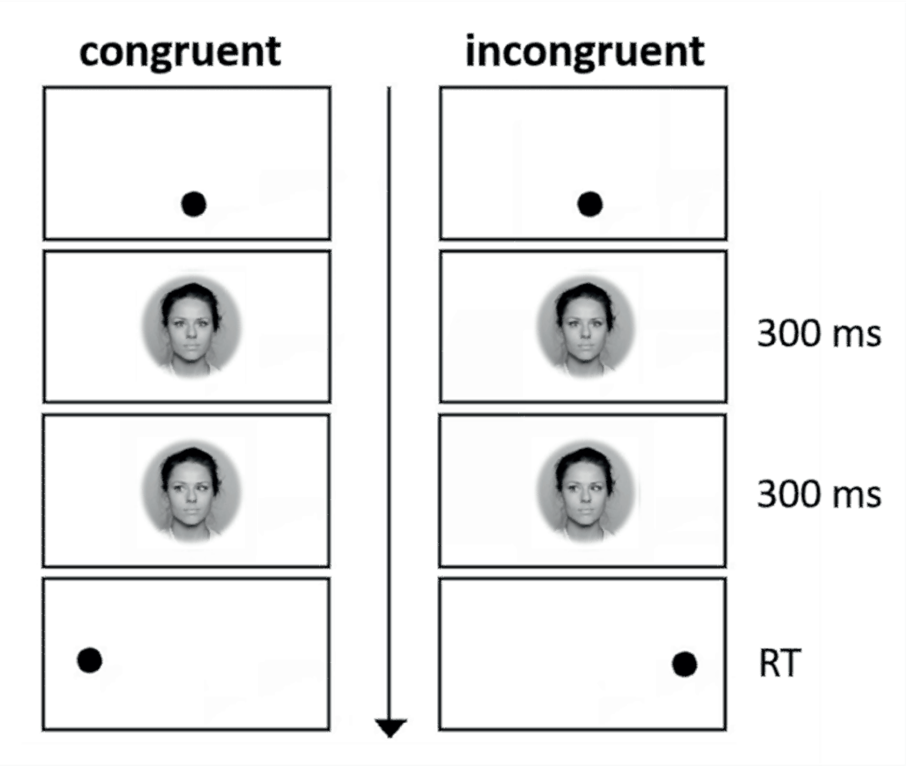

Figure 5. Schematic Outline of a Trial in the Gaze-Cuing Task. Stimuli from Oslo Face Database by Leknes Affective Brain lab (https://sirileknes.com/oslo-facedatabase/). Copyright 2014 by Leknes Affective Brain lab. Adapted with permission. RT = reaction time.

Results

Validation of Stimuli

The ordinal mixed model showed that subjects rated the central-facing stimuli classified as attractive as substantially more attractive and the stimuli classified as unattractive as less attractive (Figure 6). This effect was similar for both women (Δestimate$_{\text{attractive-intermediate}}$ = 1.81 [.34], 89% CI [1.26, 2.38], *pd* = 1.00; Δestimate$_{\text{unattractive-intermediate}}$ = −2.25 [.35], 89% CI [−2.83, −1.68], *pd* = 1.00) and men (Δestimate$_{\text{attractive-intermediate}}$ = 2.01 [.34], 89% CI [1.46, 2.54], *pd* = 1.00; Δestimate$_{\text{unattractive-intermediate}}$ = −2.25 [.35], 89% CI [−2.83, −1.68], *pd* = 1.00).

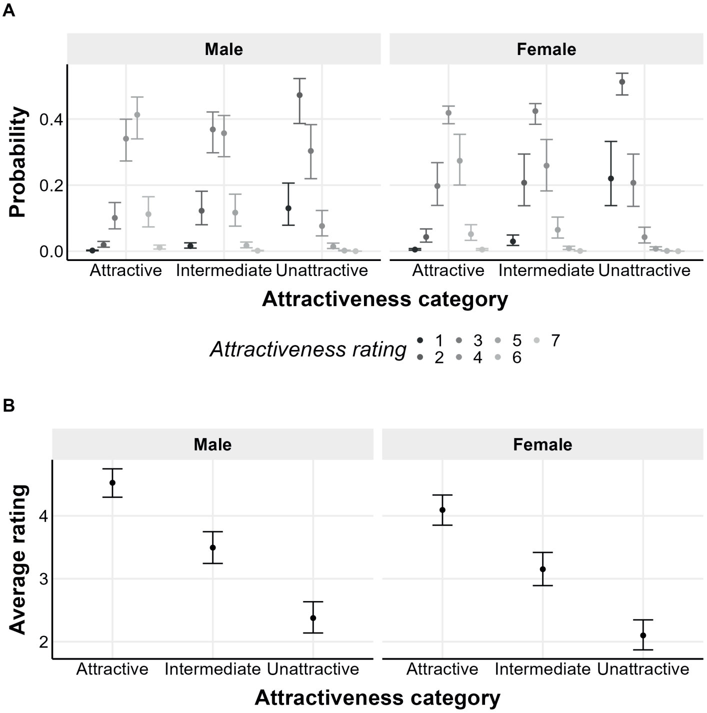

Figure 6. Validation of the Stimuli of Experiment 3. Probability of receiving high attractiveness ratings was higher for stimuli categorized as “attractive” (a). This is also depicted in (b), which treats the ratings as a continuous variable for visualization purposes.

Simple Model

To test our main prediction that attractiveness would significantly influence gaze cuing, we ran a Bayesian mixed model with by-subject mean-centered RT per trial as dependent variable and the interaction between attractiveness category and gaze congruency as independent variables (Table 3; see Appendix G for model stability c). We found a robust main effect of gaze congruency on RT (Figure 7), suggesting that people responded faster when the probe appeared on the side that was congruent with the gaze direction of the stimulus (median difference = 32.16 [1.33], 89% CI [30.01, 34.32], *pd* = 1.00).

We found no clear effect of attractiveness category on RT for congruent and incongruent trials. Specifically, on incongruent trials, there was no substantial difference in RT between attractive and intermediate stimuli (median difference = −1.68 [2.33], 89% CI [−5.39, 2.09], *pd* = .76), as well as for unattractive and intermediate stimuli (median difference= 3.22 [2.39], 89% CI [−.52, 6.92], *pd* =

.91). However, people responded slightly faster when the stimulus presented was attractive than unattractive (median difference = 4.84 [2.35], 89% CI [1.13, 8.56], *pd* = .98). Regarding congruent trials, we found no substantial difference in RT between attractive and intermediate (median difference = −.61 [2.26], 89% CI [−4.29, 3.06], *pd* = .60), unattractive and intermediate (median difference = −1.25 [2.38], 89% CI [−5.04, 2.45], *pd* = .70), or attractive and unattractive stimuli (median difference = .67 [2.36], 89% CI [−3.11, 4.37], *pd* = .61).

Table 3. Model Output for the Simple Model of Experiment 3. Note: all categorical independent variables were sum-to-zero coded.

Parameter	Median estimate	SD	89% CI lower bound	89% CI upper bound
Intercept	0.16	1.42	-2.06	2.48
Attractiveness Category [attractive]	-1.09	0.95	-2.58	0.46
Attractiveness Category [intermediate]	0.06	0.95	-1.48	1.57
Gaze Congruency [incongruent]	16.08	0.67	15.00	17.16
Attractiveness Category [attractive]: Gaze Congruency [incongruent]	-1.10	0.95	-2.59	0.44
Attractiveness Category [intermediate]: Gaze Congruency [incongruent]	-0.58	0.95	-2.07	0.96
Random effects				
sd [intercept] Trial order	9.63	1.18	7.90	11.67
sd [intercept] Subject	0.47	0.42	0.05	1.33
N_{obs} = 8425				
N_{subj} = 150				

Age and Sex

We investigated whether adding either age or sex to the model improved the predictive accuracy relative to the simple model. When comparing the model that included the three-way interaction between age, attractiveness category, and gaze congruency to the simple model, we found that the predictive accuracy of the simple model was slightly better (Δelpd_{LOO} = 4.6 [1.8]). The results were similar for the model that included the three-way interaction between sex, attractiveness category, and gaze congruency: The simple model performed slightly better than the complex model (Δelpd_{LOO} = 3.5 [2.2]). Altogether, these findings suggest that adding age or sex to the simple model did not increase the simple model's predictive accuracy.

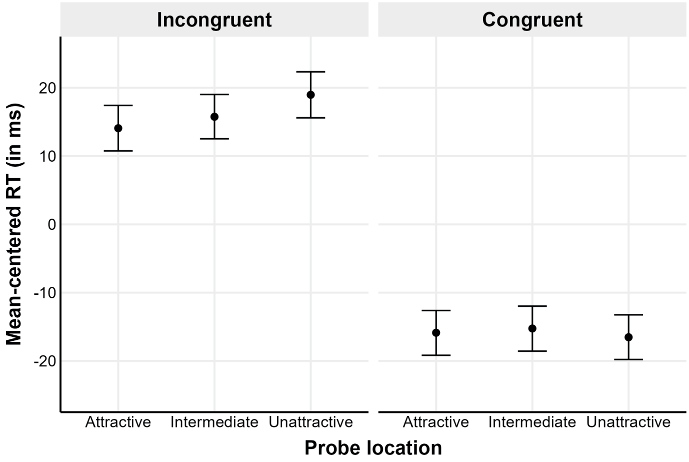

Figure 7. By-Subject Mean-Centered RTs per Condition and per Probe Location. Dots indicate the median reaction times (RT), while error bars represent the 89% credible interval. On both congruent and incongruent trials, we found no evidence for attractiveness resulting in a stronger gaze cuing effect.

Discussion

Attractiveness is a salient social signal that not only affects our judgment but also biases our attention and perception of other social information. In the current study, we investigated how facial attractiveness and symmetry modulated attention. Moreover, we investigated whether facial attractiveness modulated gaze cuing. The results show, first, that participants had an attentional bias toward attractive faces but not toward unattractive faces. Second, attention was not differentially modulated by facial symmetry. Third, gaze cuing was not affected by the attractiveness of the face. Fourth, we found no evidence for differences in attractiveness bias between men and women or between younger and older participants. These results will be discussed in more detail in the sections below.

Our first key result, that people had an attentional bias toward attractive faces, is in line with previous research (Ma et al., 2019; Ma, Zhao, et al., 2015; Maner, Gailliot, Rouby, et al., 2007). Using a similar dot-probe task as in the current study, Ma and colleagues showed that Chinese undergraduate students (*n* = 108 females: Y. Ma et al., 2015; *n* = 109 males: Y. Ma et al., 2019) had difficulties disengaging from attractive faces. While they found no overall attentional bias toward attractiveness faces, only participants who were single and primed with romantic words showed this effect. The current study builds on this work and extends it in several ways. First, we not only included the comparison between attractive and intermediately attractive faces but also included the comparison between unattractive and intermediately attractive faces. Consequently, we can conclude that participants selectively attended to attractive but not unattractive faces. This finding suggests that the attentional bias toward attractive faces is not merely the result of attractive faces deviating from the average face, as this is the case for unattractive faces as well. Second, using a large community sample with a wide age range, we were able to show that attractiveness also influences attention in Western people, regardless of their age or gender. Third, we limited the stimulus presentation duration to 300 ms to make it unlikely that participants shifted gaze once their attention had been captured by one of the two presented images (Petrova et al., 2013). Longer presentation durations allow such oculomotor shifts to occur; however, they are not recorded and thus yield noisier data (van Rooijen et al., 2017). Therefore, our results are likely to represent an attentional capture effect, while the previous studies mainly found disengagement effects. Thus, with a few methodological adjustments and a more heterogeneous sample, we were able to show that attention to attractive faces is likely a more general effect than previously assumed.

Our second key result, namely that facial symmetry does not affect implicit attention, was against our expectations. If facial symmetry were an important signal reflecting mate quality, one would expect symmetrical faces to modulate implicit attention. It is important to note that some recent studies have questioned the evolutionary importance of facial symmetry. For example, not all studies show that symmetry correlates with health (Pound et al., 2014), and symmetrical faces are more attractive even after removing symmetry information by showing only half of the face. This indicates that other factors that are correlated with symmetry may cause the high attractiveness ratings for symmetrical faces (Scheib et al., 1999). Furthermore, recent data-driven approaches to facial attractiveness have cast doubt on the importance of symmetry (Holzleitner et al., 2019; Jones & Jaeger, 2019). For example, Jones & Jaeger (2019) recently studied the differential effects of facial characteristics on the perception of attractiveness. They concluded that symmetry of facial shape is not informative when it comes to predicting attractiveness. Instead, they concluded that shape averageness is a more accurate predictor of attractiveness. Therefore, based on this perspective, we suggest that future research might study attentional biases toward averaged versus nonaveraged faces.

Our third key result, that gaze cuing was not modulated by facial attractiveness, was not in line with our prediction. We did find a strong cuing effect, but this effect was seemingly unaffected by attractiveness category of the stimuli, as participants did not respond faster on congruent trials in the Posner paradigm when attractive faces were displayed. Our findings contradict previous literature describing the effect of evolutionarily relevant facial characteristics on gaze cuing (Deaner et al., 2007; Hori et al., 2005; Jones et al., 2010; Ohlsen et al., 2013). Given that attractiveness is such an important criterion for partner choice, it is surprising that gaze cuing was not modulated by facial attractiveness. One likely explanation is methodological: Jones et al. (2010) found a significant effect of facial dominance on gaze cuing when side-looking stimuli were presented for 200 ms but not when they were presented for 400 ms or 800 ms. On the contrary, in our study, we used a presentation duration of 300 ms. Thus, it might be the case that the subtle effect of facial attractiveness on reflexive gaze following manifests itself only at very short presentation durations. Furthermore, the current gaze-cuing paradigm allows for only indirect inference of the isolated effect of attractiveness on gaze cuing. However, this paradigm does not provide any information about how a person would behave in a situation where people varying in attractiveness look in different directions. In this scenario, would the person shift their gaze in congruence with the most attractive person or not? To answer this question, we believe that an approach that combines the dot-probe and gaze-cuing paradigm has its merits. Such a paradigm would help to further elucidate the link between attractiveness and gaze cuing.

One important limitation of our study is the lack of data on motivation of the participants with regard to mate searching. This could possibly explain the null effects that we found in Experiments 2 and 3. Previous work has suggested that motivations might affect implicit cognition in partner choice contexts (Maner & Ackerman, 2015). Consequently, empirical studies have found that attentional biases for attractive faces do not always generalize to all people. For example, attentional biases for attractive faces might only become apparent in people with a short-term mating strategies (Maner, Gailliot, & DeWall, 2007; Maner, Gailliot, Rouby, et al., 2007) or in participants who are not in a romantic relationship (Ma et al., 2019; Ma, Zhao, et al., 2015). It is theoretically possible that people who are motivated to find a partner are more likely to show an implicit attentional bias for symmetrical faces, for example. In line with this idea, sociosexuality predicted explicit preferences for symmetrical male faces in women (Quist et al., 2012). Therefore, we want to emphasize the need for future studies to incorporate relationship status and measures of sociosexuality when investigating implicit cognition. The same applies to context-dependent gaze cuing; while we did not find evidence that attractive opposite-sex faces enhance gaze cuing, this does not rule out such an effect in other mate choice contexts. For example, people might follow the gaze of attractive same-sex conspecifics in a mate choice context to identify which opposite-sex individuals they attend to. Such explicit mate choice copying has been described for both men and women (Place et al., 2010; Waynforth, 2007), but future work could establish whether this generalizes to implicit gaze cuing. Thus, incorporating individual motivations and exploring different mate choice contexts might help to further elucidate the effect of attractiveness on implicit cognition.

Importantly, we found no effect of sex on bias toward attractiveness in either of the experiments. Our findings are in line with what (Maner et al., 2003) call the *opposite-sexed beauty captures the mind* hypothesis and contrast with the *one-sided gender bias* hypothesis. Thus, both men and women in our study seemed to selectively focus on attractive opposite-sex faces. Similarly, we found no effect of age group on attractiveness bias: Participants of both reproductive and postreproductive age had a similar bias toward attractive faces. Taken together, these results suggest that the effect of attractiveness on social cognition generalizes over sex and age. However, studies using a clear mate search context are necessary to confirm these findings.

In conclusion, our findings corroborate previous research on attractiveness bias by showing an implicit attentional bias toward attractive faces, likely reflecting an attention capture effect, in a Western sample with a wide age range. Thereby, our results demonstrate how facial attractiveness, a characteristic that is highly relevant from an evolutionary perspective, affects implicit social cognition. However, we did not find an effect of attractiveness on gaze cuing. Nevertheless, we believe that incorporating individual motivations and applying more ecologically valid paradigms can help to further elucidate the link between attractiveness and gaze cuing.

Chapter 5

Individual attractiveness preferences differentially modulate immediate and voluntary attention

Abstract

Physical attractiveness plays a crucial role in mate choice for both men and women. This is reflected in visual attention: people immediately attend towards and look longer at attractive faces, especially when they are motivated to find a partner. However, previous studies did not incorporate real-life dating decisions. Here, we aimed to combine attentional tasks with individual attractiveness ratings and a real-life mate choice context, namely a speed-dating paradigm. We investigated whether heterosexual non-committed young adults showed biases in immediate and voluntary attention towards attractive faces and preferred dating partners. In line with previous research, we found considerable individual differences in individual attractiveness preferences. Furthermore, our results showed that men had a bias towards attractive faces and preferred dating partners in the immediate attention task, while results for women were mixed. In the voluntary attention task, however, both men and women had an attentional bias towards attractive faces and preferred dating partners. Our results suggest that individual attractiveness preferences are good predictors of especially voluntary attention. We discuss these findings from an evolutionary perspective and suggest directions for future research.

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/AWSZSB.

Introduction

Physical attractiveness permeates important aspects of human interaction and shapes our judgements about people. Previous research shows that people associate positive personality traits with attractive people (Dion et al., 1972; Griffin & Langlois, 2006) consider them more cooperative (Andreoni & Petrie, 2008), and attractive people have even been shown to fare better in the labor market (Maestripieri et al., 2017; Nault et al., 2020). In addition, physical attractiveness has an important influence on mate choice, and its weight in shaping mate choice has important effects in fundamental aspects of our psychology, such as attention. For example, previous research has shown that people's attention is drawn faster and for a longer duration to attractive stimuli (Leder et al., 2016; Lindell & Lindell, 2014). However, given that human mate choice is such a fundamentally complex and multifaceted phenomenon, researchers have treated it in a wide variety of distinct approaches that may capture only some of said complexity. For example, human mate choice has been studied by focusing on cognitive processes (Maner & Ackerman, 2015; Roth et al., 2022; Todd et al., 2007), attractiveness ratings (Asendorpf et al., 2011; Roth, Samara, & Kret, 2021), and real-life interactions (Eastwick & Finkel, 2008; Perilloux et al., 2012; Prochazkova et al., 2022). Even though previous studies have integrated multiple methods to investigate mate choice, no previous study has examined the influence of attractiveness on visual attention and linked this to decisions in a realistic mate choice context. Given the context-sensitivity of cognitive processes (Kenrick et al., 2010), we explore how individual attractiveness preferences and partner preferences shape our immediate and voluntary attention using a novel setting. Specifically, here, we combine well-established cognitive tasks with attractiveness rating tasks and a speed-date paradigm to examine whether and how these different approaches to studying human mate choice concord.

Physical attractiveness is strongly associated with attraction to a mate (Luo & Zhang, 2009; Roth, Samara, & Kret, 2021), and both women and men mention physical attractiveness as an important criterion for mate selection (Buss & Barnes, 1986; Rhodes, 2006). Consequently, physically attractive people have more sexual partners (Karraker et al., 2017) and a higher reproductive success (Jokela, 2009). From an evolutionary perspective, attractiveness has been proposed to be a cue of genetic quality in terms of health or fertility: by selecting an attractive partner, one can increase the likelihood of bearing offspring with high genetic quality

(Rhodes, 2006; Thornhill & Gangestad, 1999). Some studies indeed suggest that attractiveness is positively correlated with health (Mengelkoch et al., 2022; Nedelec & Beaver, 2014), although this has been heavily debated (Cai et al., 2019; Jones et al., 2021; Pátková et al., 2022). Accordingly, people rate attractive faces as healthier than unattractive faces (Rhodes et al., 2007), although this could be the result of a general halo effect for attractive people (Dion et al., 1972; Kalick et al., 1998). Altogether, by selecting an attractive mate, humans might confer their offspring a selective advantage, thereby increasing their reproductive success.

If selecting a physically attractive mate indeed results in greater fitness, this may be reflected in specific cognitive mechanisms that help people to identify, and feel attracted to, physically attractive mates. Some of these mechanisms may be understood as perceptual biases, previously termed sexually selective cognition (Maner & Ackerman, 2015). These biases have been shown to interact with different cognitive processes. For example, men and women will exert more effort to see pictures of attractive than unattractive opposite-sex stimuli (Hayden et al., 2007), although this opposite-sex bias is especially strong in men (Levy et al., 2008). When it comes to recognition memory, people seem to specifically remember attractive faces (Lin et al., 2020; Marzi & Viggiano, 2010). Importantly, this memory bias seems to be strongest for young participants, who are at the age where they are most likely to start getting involved in romantic interactions (Lin et al., 2020). These examples show how attractiveness can modulate human cognition.

Apart from effort and memory biases, the majority of experimental studies on cognition and mate choice have focused on processes of visual attention. Several studies show attentional biases towards physically attractive faces: they are attended to first and hold our attention for a longer time (Lindell & Lindell, 2014). Physically attractive faces are also preferentially attended to in preferential looking paradigms (Leder et al., 2016; Mitrovic et al., 2018). When it comes to immediate attention, previous work has shown that people identify faces that were previously rated as attractive extremely quickly. For example, when presented with two pictures at the same time for 100 ms, participants could select the most attractive picture above chance level (Guo et al., 2011). In addition, using a dot-probe paradigm with a slightly longer time scale of 300 ms, Roth et al. (2022) demonstrated that participants showed an attentional bias towards attractive faces paired with intermediately attractive faces, but not towards unattractive faces paired with intermediately attractive faces. However, it should be noted that attractiveness categories were predefined based on ratings by a different participant sample in this study (Ma, Correll, et al., 2015).

Such an approach is typical in studies investigating attractiveness, where traditionally researchers have focused on average ratings of general attractiveness. This approach is based on the notion that people strongly agree on which features and characteristics are attractive (Langlois et al., 2000). However, recent research has emphasized that it is important to disentangle shared and idiosyncratic contributions to judgments (Martinez et al., 2020) because ample evidence shows that beauty is—at least partly—in the eye of the beholder, as agreement on attractiveness is about 50% (Bronstad & Russell, 2007; Hönekopp, 2006). Importantly, such individual preferences can also influence date success, i.e., willingness to meet again after a first date (Baxter et al., 2022). These inter-individual variations are possibly the result of differences in environments (Germine et al., 2015), such as culture (Zhan et al., 2021) and close social relationships (Bronstad & Russell, 2007). Nevertheless, most traditional laboratory studies did not take idiosyncratic preferences of participants into account, even though there can be considerable inter-individual variation in judging attractiveness. Taking these individual differences into consideration might reveal more pronounced effects of attractiveness on cognition. Thus, in the present study, we aimed to examine whether and the manner in which idiosyncratic attractiveness preferences influence immediate attention.

When it comes to voluntary attention, that is, where attention is allocated when able to do so freely, multiple studies have found that participants focus their attention on their sex of interest, or on the most attractive person of their sex of interest, depending on the design. For instance, Dawson & Chivers (2016, 2018) presented sexually explicit stimuli to participants that contained same-sex or opposite-sex people and found that heterosexual participants fixated more on the opposite-sex stimuli. Mitrovic et al. (2016)extended these findings by presenting same-sex and opposite-sex stimuli varying in attractiveness to heterosexual and homosexual participants. They found that participants attended most to the attractive faces corresponding to their sexual preference. Follow-up studies modified this paradigm by using the participants' own attractiveness ratings of the stimuli, instead of predefining stimuli as attractive or unattractive, and yielded similar results: people spent more time looking at faces that they found attractive (Leder et al., 2016; Mitrovic et al., 2018). Thus, a plethora of studies shows that people selectively attend to the more attractive face they are presented with.

Cognition can be substantially influenced by top-down processes (Kenrick et al., 2010, 2010), and attentional biases related to mate choice are no exception to this. More specifically, mating motivations seem to modulate attentional processing of attractiveness. For example, Y. Ma et al. (2015, 2019) used a dot-probe paradigm with 500 ms presentation duration to study whether immediate attention was modulated by attractiveness and relationship status. They found that non-committed participants' attention was captured by attractive faces the most, and that these same participants had trouble disengaging from attractive facial stimuli. When it comes to voluntary attention, similar results have been found: non-committed participants showed a stronger positive correlation between perceived physical attractiveness and attention than committed participants (Mitrovic et al., 2018). This suggests that the bias towards physical attractiveness is especially pronounced when it is adaptive, i.e., for people that might be looking for a partner.

It has been suggested that men are more attuned to physical attractiveness than women (Buss, 1989). This has been supported by questionnaire studies, where women seem to place less emphasis on physical attraction of their partner than men do (Bech-Sørensen & Pollet, 2016). This is also reflected in cognition: men show a stronger correlation between stimulus attractiveness and preferential looking (Mitrovic et al., 2018). Similar patterns have been found in immediate attention studies (Maner, Gailliot, & DeWall, 2007; Zhang et al., 2017), although this finding is not always replicated (Roth et al., 2022). However, these sex differences do not always become apparent in studies that investigate real-life interactions. On the contrary, both women and men seem to rely mostly on physical attractiveness of their partners to make mate choice decisions during speed-dates (Eastwick & Finkel, 2008; Luo & Zhang, 2009; Roth, Samara, & Kret, 2021). Thus, while some studies report sex differences in attractiveness bias in attentional paradigms, these differences do not seem to be reflected in dating decisions. This raises the question whether these different approaches to studying mate choice capture the same processes and to what extent they are actually informative with regard to real-life mate choice.

Here, we therefore combined two paradigms that have been used frequently to study immediate and voluntary attention in the context of human mate choice with a realistic paradigm to study human mate choice, namely speed-dating. More specifically, we investigated the association between individual preferences for attractiveness and date outcome, respectively, on immediate and voluntary attention in non-committed young adults. To test immediate attention, we employed a dot-probe task (MacLeod et al., 1986). In the dot-probe task, participants briefly view two pictures presented on the display, one of which is then replaced by a dot. Participants are asked to indicate the location of the dot (right vs. left) using the corresponding keyboard keys. To investigate voluntary attention, we used a preferential looking task, where participants can freely view two stimuli in each trial (Leder et al., 2016), while their eye movements were recorded with an eye tracker. We combined these two cognitive tasks with a speed-date paradigm in order to create a realistic mate-choice context. Speed-dating has been shown to have strong ecological validity, as participation in a speed-dating experiment can translate into real-world romantic relationships (Finkel et al., 2007). Furthermore, we aimed to examine how the results of two different but well-established types of paradigms (i.e., speed dating and cognitive tasks) relate to each other. This is because these two pervasive paradigms may be capturing fundamentally different processes relevant to mate choice that are, nonetheless, relevant to understanding the role of perceived attractiveness. As such, we believe the integration of these paradigms has the potential to more holistically inform the complex phenomenon that is human mate choice.

Our study aimed to contribute to the understanding of the interplay between cognition, attractiveness, and mate choice in two main ways. First, we linked idiosyncratic attractiveness preferences not only to voluntary, but also immediate attention. Second, we studied whether attractiveness-related attentional biases are indeed reflective of actual mate choice. Regarding our analyses, we first explored whether there were idiosyncratic differences in attractiveness ratings in our sample, as reflected in inter-rater reliability of attractiveness ratings. With regards to individual attractiveness preferences and the dot-probe task, we expected that participants would respond faster to the dot when it replaced a picture they themselves had previously rated as highly attractive; whereas they would respond slower to the dot when the distractor was a picture they had rated as highly attractive. With regards to date outcome and the dot-probe task, we expected people to respond faster to the dot when it replaced a picture of a person they later felt attracted to on a speed-date. However, we expected them to respond slower when the distractor was a picture of a person they later felt attracted to while on a speed-date. With regard to individual attractiveness preferences and preferential looking, we expected a positive association between individual attractiveness rating and looking time. Furthermore, regarding date outcome and looking time, we expected participants to look longer at people they later felt attracted to on a speed-date. For each analysis, we also explored whether the relationships would be more pronounced for men than for women.

Method

Participants

Eighty (*N* = 80) participants were recruited for a speed-dating event and divided into four groups of 10 male and 10 female participants. In line with the inclusion criteria, all participants reported that they were between 18 and 26 years old, heterosexual, non-committed, Dutch-speaking, and not under treatment for psychiatric disorders. All but 2 participants indicated that they were interested in pursuing a long-term relationship. Ten participants did not attend the experimental session and three participants (1 woman) withdrew their participation before the speed-dating sessions, leading to a final sample of 67 (*N* = 67; 35 women: *M*age = 22.03, *SD* = 2.26; men: *M*age = 22.61, *SD* = 1.75). All participants provided informed consent in accordance with the declaration of Helsinki. Participants received a complementary ticket to Apenheul Primate Park (Apeldoorn, the Netherlands) for their participation. The study was approved by the Leiden University Ethics Committee (CEP: 2020-02-20-M.E.Kret-V1-2169).

Procedure

After filling in several demographic questionnaires, the researchers took profile photos of the participants against a white background and also collected auditory and olfactory material, which will not be described in this paper. Hereafter, all participants completed a battery of cognitive tasks (preregistered using the AsPredicted database 36,394). Here, we focus on the dot-probe, preferential looking task, and attractiveness rating task. All tasks were controlled by an E-prime script (E-prime version 3; Psychology Software Tools, Pittsburgh, PA) in conjunction with the E-Prime Extensions for Tobii Pro (EET) for the preferential looking task. All stimuli were presented against a gray background. Furthermore, all tasks were presented on an 23.8-inch HP EliteDisplay 243 m monitor with 1680 × 1050 resolution and 60 Hz refresh rate.

In the dot-probe task, participants briefly view two pictures of the presented on the display, one of which is then replaced by a dot. Participants are asked to indicate the location of the dot (right vs. left) using the corresponding keyboard keys. In our study, all stimuli consisted of the opposite-sex participants' profile photos from the same group. In the case that one group consisted of fewer than 10 individuals, pictures of opposite-sex participants from the previous group were added to keep the number of trials consistent across participants. It is important to note that participants had not met their partners at that point in the experimental procedure and thus could not have known that these were replacement pictures. Each trial started with a centrally presented fixation cross for a jittered duration between 1020 and 1260 in increments of 60 ms. Next, participants viewed the pictures of two opposite-sex participants for 300 ms, one of which was then replaced by a dot until the participant indicated the correct location using the corresponding keyboard keys (*z* for left, *m* for right). Every trial ended with an inter-trial interval between 1380 and 1620 ms in increments of 60 ms. After completing 10 practice trials, participants viewed all possible combinations of the opposite-sex participants' photos (i.e., 45 dyads) twice, so each participant in a dyad would be presented as the probe (i.e., the picture replaced by the dot) and the distractor picture (i.e., the picture not replaced by the dot) leading to a total of 100 trials. Location of the probe and distractor pictures was pseudo-randomized across the trials. The task lasted approximately 8 min.

In the preferential looking task, in each trial, participants viewed two of the opposite-sex participants' pictures while their eye movements were recorded using an X2-60 Tobii eye-tracker (Tobii Pro, 2014) at a sampling rate of 60 Hz. Participants placed their chin on a chin rest at approximately 50 cm from the monitor. Each trial started with a centrally presented fixation cross for 720 ms, followed by the two pictures presented on the display for 3000 ms. Similar to the dot-probe task, in the case that one group consisted of fewer than 10 individuals, pictures of opposite-sex participants from the previous group were added to keep the number of trials consistent across participants. Every trial ended with a jittered ITI between 1380-1620 ms in increments of 60 ms. After performing 3 practice trials, participants completed 45 trials. The task lasted approximately 6 min.

In addition to the tasks described above, participants rated the attractiveness of all of the stimuli on a 7-point scale. The stimuli were presented sequentially for 3 s on a computer monitor, after which the participants could indicate how attractive they found the person in the stimulus. The order of the tasks was randomized between participants.

After completing the tasks, participants went on a maximum of ten 4-min speed-dates (Lee et al., 2020; Perilloux et al., 2012). Men and women were seated at opposite sides of a table, their view of their partner occluded by a barrier. At the start of each date, the barrier was removed, and following the ring of the bell, participants had a four-minute date with their partner. After 4 min, participants indicated the date outcome, i.e., whether they would be interested in going on another date with them (yes/no); their prediction about whether their partner would be interested to go on another date with them (yes/no); and whether they knew their partner before the date (yes/no). Furthermore, we asked participants to indicate how attractive they found their partner (7-point scale) and how attractive they considered them as a long-term mate (7-point scale). It should be noted that these questions referred to attractiveness in general, and not specifically physical attractiveness. Participants had one minute to fill in the questionnaire after each date. Next, male participants rotated to their next prospective partner. After completing all possible date combinations, participants were debriefed about the purposes of the study.

Data processing

Dot-probe

In total, 58 participants completed the dot-probe task. In the second female group, we could not collect dot-probe data due to a technical issue. In total, we had 5220 datapoints for the dot-probe task before data filtering. One participant did not complete the pre-date attractiveness rating task. Therefore, we excluded this participant's data (90 trials) from the analysis that investigated the effect of attractiveness on immediate attention, leaving us with data from 57 participants. Next, we excluded outliers by subject: as a lower boundary, we used 200 ms for anticipatory reaction times (Whelan, 2008). We calculated the upper limit by subject following Leys and colleagues (Leys et al., 2013): we calculated the median absolute deviation (MAD) per subject and the median RT per subject. We then used a moderately conservative criterion to exclude trials: if the RT was slower than the subject's median RT + 2.5 * MAD, we excluded the trial. These outlier criteria resulted in the exclusion of 299 trials (5.83%). Hereafter, we centralized the RTs by subject. This was done to make it easier to set a prior for the Intercept. All factorial predictors were sum coded, and pre-date attractiveness ratings were centered at 4 because this was the middle option.

We followed a similar procedure for the analysis that investigated the association between date outcome (i.e., willingness to go on another date with dating partner) and post-date attractiveness rating on immediate attention. Two participants dropped out before the speed-date part of the experiment. Therefore, we had to exclude their data, leaving us with data from 56 participants. Some participants did not go on a speed-date with every opposite-sex person they saw on the stimuli, either due to dropouts or unequal group size. After excluding the cases where date outcomes were missing for either the probe or the distractor stimulus, we ended up with 3460 data points out of the original 5220. Hereafter, we again excluded outliers by subject (see above), resulting in the exclusion of 209 trials (6.04%).

Eye-tracking

In total, 36 participants completed the eye-tracking task. One participant did not complete the pre-date attractiveness rating task and did not participate in the speed-dates. Therefore, we excluded their data (45 trials) from the analysis. Furthermore, we excluded 6 trials because participants were not looking at the stimuli, leaving us with 1569 trials from 35 participants to investigate the effect of attractiveness on voluntary attention. For the analysis that investigated the effect of date outcome and post-date attractiveness rating on voluntary attention, we had a smaller number of trials due to the fact that not all people that were rated for attractiveness participated in the speed-dates (either due to dropout or due to unequal group sizes). In total, we could include 1009 trials from 35 participants.

Eye-tracking data were recorded continuously throughout the task with a sampling rate of 60 Hz. Here, only data during the stimulus presentation were analyzed. Fixations on either area of interest (AOI) were logged using a custom E-prime script. We excluded practice trials (6.25%) and gaze samples where either the left or right pupil was not recorded (3.50%). Following these criteria, we were left with 90.25% of the data intact.

Statistical analyses

All analyses were performed in R statistics Version 4.1.3 (R Core Team, 2022). First, we calculated the Intra-Class Correlations (ICC) for the individual pre-date attractiveness ratings. We used the R package *irrNA* (Brueckl & Heuer, 2022), because it properly deals with missing values in the computation of ICC. In line with recommendations from McGraw & Wong (McGraw & Wong, 1996) we used the ICC(A, 1) to test for absolute agreement between rates. We report the ICC estimate and the 95% confidence interval.

Furthermore, we used the R package *correlation* (Makowski et al., 2020) to test the relationship between pre-date attractiveness ratings, post-date attractiveness ratings, and date outcome. The *correlation* package allows for computation of a wide variety of correlations, such as Bayesian multilevel correlations. In our case, we used Bayesian multilevel Spearman correlations to investigate the association between pre-date and post-date attractiveness ratings. To test the relationships between date outcome and pre-date and post-date attractiveness ratings, respectively, we used Bayesian point-biserial correlations. These analyses were based on a dataset that consisted of only complete cases for all three variables of interest. In total, this concerned 482 datapoints of 58 participants.

For our main analyses, we used Bayesian mixed models. Bayesian analyses have gained in popularity over the past few years because they offer a number of benefits compared to frequentist analyses (Kruschke et al., 2012; Makowski et al., 2019). While frequentist methods (e.g., *p*-value null-hypothesis testing; Wagenmakers, 2007) inform us about the credibility of the data given a hypothesis, Bayesian methods inform us about the credibility of our parameter values given the data that we observed. This is reflected in the different interpretation of frequentist and Bayesian confidence intervals: The first is a range of values that contains the estimate in the long run, while the latter tells which parameter values are most credible based on the data (Kruschke et al., 2012; McElreath, 2018). Furthermore, Bayesian methods allow for the inclusion of prior expectations in the model, are less prone to Type I errors, and are more robust in small and noisy samples (Makowski et al., 2019). Altogether, these reasons make Bayesian methods a useful tool for data analysis.

All models were created in the Stan computational framework and accessed using the *brms* package (Bürkner, 2017, 2018) , version 2.17.0. All models were run with 4 chains and 5000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van de Schoot, 2017). We found no divergences or excessive autocorrelation in any model.

Dot-probe

To analyze the dot-probe data we used Bayesian mixed models with a Gaussian distribution. First, to study the association between attractiveness and immediate attention, we modeled *Reaction time* (mean-centered by subject) as a function of *Attractiveness rating of probe picture* and *Attractiveness rating of distractor picture*, and their interactions with *Gender*. We allowed the intercept and the effects of *Attractiveness rating of probe picture* and *Attractiveness rating of distractor picture* to vary by *Subject.* Second, to study the association between date outcome (i.e., willingness to go on another date with dating partner) and immediate attention, we followed the same procedure as described above. However, the predictors *Attractiveness rating of probe picture* and *Attractiveness rating of distractor picture* were replaced with *Date again probe picture* (binary: yes/no) and *Date again distractor picture* (binary: yes/no), also in the random effect formula.

We used a Gaussian prior with $M=0$ and $SD=2.5$ for the Intercept of the model. For the independent variables, we specified regularizing Gaussian priors with $M=0$ and $SD=5$. For all variance parameters, we kept the default Student's t priors with 3 degrees of freedom. After running the models, we used the *emmeans*-package (Lenth, 2022) to obtain estimates and pairwise contrasts based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects. First, we report the median estimate *b,* and median absolute deviation of the estimate between square brackets. Second, we report an 89% credible interval of the estimate (89% CrI). We have chosen 89% instead of the conventional 95% to reduce the likelihood that the credible intervals are interpreted as strict hypothesis tests (McElreath, 2018). Instead, the main goal of the credible intervals is to communicate the shape of the posterior distributions. Third, we report the probability of direction (*pd*), i.e., the probability of a parameter being strictly positive or negative, which varies between 0.5 and 1 (Makowski et al., 2019).

Eye-tracking

To analyze the eye-tracking data, we used a zero–one inflated beta model, which is suitable for continuous proportions containing zeros and ones. These models consist of two components, namely a beta component to describe the values between 0 and 1, and a binary component to predict the occurrences of zeros and ones (Ospina & Ferrari, 2012). For each trial we calculated a *Looking time bias score* by dividing the time fixating on the left picture by the total time fixating on the pictures. Thus, this score reflects the proportion of fixation time spent looking at the left picture. In looking time studies, it is common practice to calculate a looking time bias (proportion of total looking time). In the case of clear categories, this is no problem. For example, imagine a study where one examines attention to attractive vs. unattractive faces. One could calculate a looking time bias by calculating the proportion of time looking at the attractive face for all trials. However, in our case, we have no categorical variables but continuous ones, namely attractiveness ratings. Thus, we cannot calculate an informative bias like in the example above. Therefore, we have used the location of the photos as a reference point to calculate the looking time bias, by calculating the bias toward the left picture. Hereafter, we have tested whether this bias is affected by (1) the attractiveness ratings of the left and right picture, and (2) date outcome.

To study the association between attractiveness and voluntary attention, we modelled *Looking time bias score* (proportion of time looking at the left picture) as a function of *Attractiveness rating of the left picture* and *Attractiveness rating of the right picture*, and their interactions with *Gender*. We allowed the intercept to vary by *Subject*. Importantly, we weighed each trial by the looking time in that trial relative to the subject's average (see Data Processing). Thus, trials in which the participant paid more attention to the screen had a larger weight in the analysis. In this manner, we avoided that trials where participants were distracted or disinterested would have a large influence on the outcome of our analysis. Furthermore, we specified the same formulas for the precision parameter (*phi*; shape of the beta distribution), the zero–one inflation parameter (*zoi*; probability of observing a zero or a one), and the conditional one-inflation parameter (*coi*; probability of observing a one if a zero or one is observed). To study the association between date outcome (i.e., willingness to go on another date with dating partner) and voluntary attention, we followed the same procedure as described above. However, the predictors *Attractiveness rating of the right picture* and *Attractiveness rating of the left picture* were replaced with *Date again right picture* (binary: yes/no) and *Date again left picture* (binary: yes/no).

We used a Gaussian prior with $M = 0$ and $SD = 0.25$ for the Intercept of the beta component of the model. For the independent variables, we specified regularizing Gaussian priors with $M = 0$ and $SD = 0.5$. This also applied to the independent variables in the formulas for *phi, coi,* and *zoi*. For all variance parameters, we kept the default Student's *t* priors with 3 degrees of freedom. Furthermore, we kept the default logistic priors for the Intercepts of *zoi* and *coi*, and default Student's *t* prior with 3 degrees of freedom for the Intercept of *phi*.

After running the models, we used the *emmeans*-package (Lenth, 2022) to integrate the different model components, and provide estimates based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects (see Statistical analyses; Dot-probe). It is important to note, though, that the predictions are on the response scale (probability). This complicates interpretation for the continuous variables, because the slope on the response scale is not constant but is shallower or steeper depending on the value of the continuous variable. In the text we report the effect size measures for when the continuous variable of interest is set at 0, but in the Supplementary Material we provide similar measures for other values of the continuous variable of interest.

Model comparisons

For both the dot-probe and eye-tracking analyses, we additionally created a complete cases dataset in which we included only those cases for which we had pre-date attractiveness ratings, post-date attractiveness ratings, and date outcomes. Using these two datasets, we again ran the analyses described above (with pre-date attractiveness, post-date attractiveness, or date outcome as predictor, respectively). Hereafter, we used leave-one-out cross validation (PSIS-LOO-CV: Vehtari et al., 2017) to calculate the expected log predictive density (elpd_{LOO}), which quantifies predictive accuracy for each model. Then, we calculated the difference in elpd_{LOO} ($\Delta\text{elpd}_{\text{LOO}}$) between all three models. If $\Delta\text{elpd}_{\text{LOO}}$ of two models is at least two SEs, this suggests that the models substantially differ in predictive performance (Johnson et al., 2022). Therefore, we report both the $\Delta\text{elpd}_{\text{LOO}}$ and the SE of the difference. In total, the immediate attention dataset consisted of 3198 trials of 55 participants, while the voluntary attention dataset consisted of 1009 trials of 35 participants.

Results

Inter-rater agreement on attractiveness

When examining the inter-rater agreement on pre-date attractiveness ratings, we found an ICC(1, A) of 0.42 (95% CI [0.32; 0.52]). This result suggests that participants differed in their attractiveness preferences independent of gender. Furthermore, we explored the inter-rater agreement for men and women separately. For women, we found an ICC(1, A) of 0.25 (95% CI [0.14; 0.41]), while for men, we found an ICC(1, A) of 0.50 (95% CI [0.39; 0.64]). These results suggest that women had substantially lower agreement than men.

Correlations between attractiveness ratings and date outcome

We found that pre-date attractiveness rating, post-date attractiveness rating, and date outcome all showed a strong correlation. First, a point-biserial correlation indicated that pre-date attractiveness rating and date outcome were correlated ($r = 0.44$, 89% CrI [0.36; 0.50], $pd_+ = 1.00$). Second, we found that post-date attractiveness showed an even stronger correlation with date outcome ($r = 0.67$, 89% CrI [0.62; 0.71], $pd_+ = 1.00$). Third, a Spearman correlation showed that pre-date and post-date attractiveness were correlated ($r = 0.57$, 89% CrI [0.51; 0.62], $pd_+ = 1.00$).

Immediate attention (dot-probe)

Pre-date attractiveness ratings

We first examined the association between *Pre-date attractiveness rating* and *Reaction time* using a Bayesian mixed model with Gaussian distribution (Supplementary Table 1; see Appendix G for model stability checks). We found a robust overall effect of *Pre-date attractiveness rating of distractor picture* on *Reaction time* ($b = 1.46$ [0.53], 89% CrI [0.60; 2.29], $pd_+ = 1.00$), with participants responding slower by 1.46 ms to the probe when there is an increase of 1 in attractiveness ratings of the distractor picture. There was no robust interaction with *Gender* ($b_{\text{women-men}} = -0.83$ [1.06], 89% CrI [− 2.49; 0.88], $pd_- = 0.79$). However, after visually inspecting the results, we wanted to explore whether the positive effect of *Pre-date attractiveness rating of distractor picture* on *Reaction Time* was robust within each level of *Gender.* We found that the effect was indeed robust for men ($b_{\text{men}} = 1.87$ [0.65], 89% CrI [0.80; 2.88], $pd_+ = 1.00$), but not for women ($b_{\text{women}} = 1.04$ [0.83], 89% CrI [− 0.33; 2.34], $pd_+ = 0.89$). Thus, men responded slower to the probe by 1.87 ms when the attractiveness rating of the distractor picture was increased by 1, while no robust effect was found for women (Figure 1 top panel).

Furthermore, we found a robust overall effect of *Pre-date attractiveness rating of probe picture* on *Reaction time* ($b = -1.11$ [0.55], 89% CrI [− 1.97; − 0.24], $pd_- = 0.98$), whereby participants responded faster by 1.11 ms when the attractiveness rating for the probe picture was increased by 1. In this case, however, the effect was modulated by *Gender* ($b_{\text{women-men}} = 2.83$ [1.06], 89% CrI [1.12; 4.51], $pd_+ = 1.00$).

Therefore, we further explored the slope per *Gender.* We found a robust negative effect of *Pre-date attractiveness rating of probe picture* for men (b_{men} = − 2.51 [0.67], 89% CrI [− 3.59; − 1.48], pd_{-} = 1.00), indicating that men responded faster by 2.51 ms when the attractiveness rating of the probe picture was increased by 1. For women, on the other hand, we found no robust effect (b_{women} = 0.30 [0.85], 89% CrI [− 1.03; 1.59], pd_{+} = 0.64). Thus, men seemed to respond faster to the probe when they considered the image that was replaced by the probe highly attractive, while no robust effect was found for women (Figure 1 lower panel).

We performed the same analysis with the *Post-date attractiveness ratings* as predictor. This analysis yielded the same results (Supplementary Table 2).

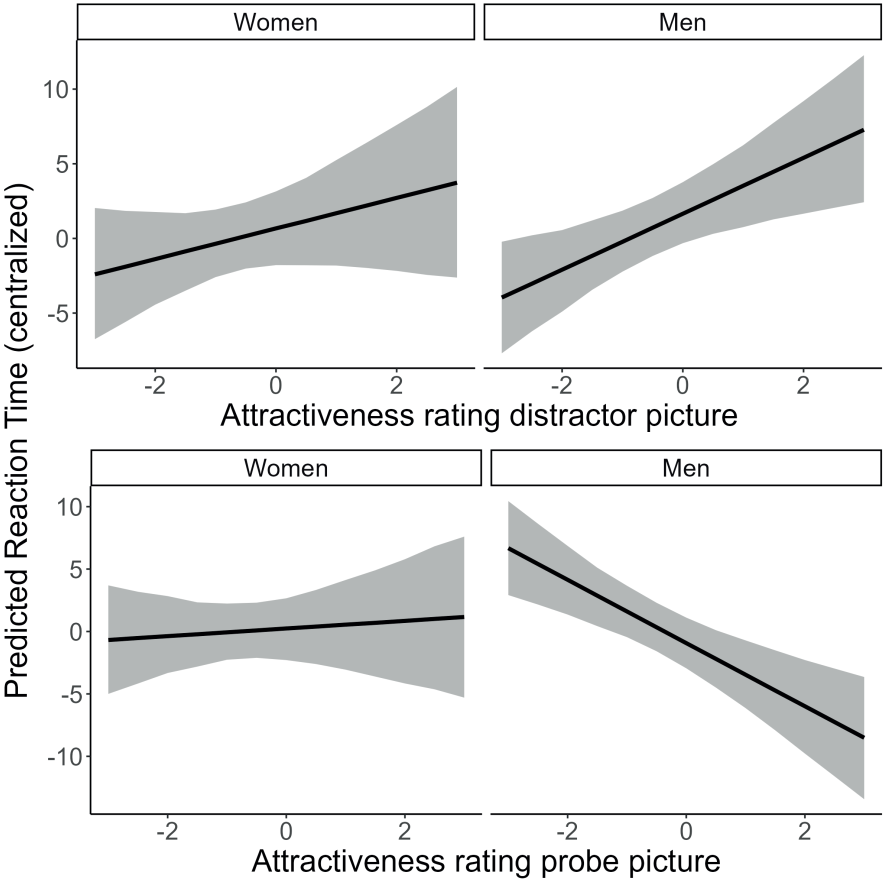

Figure 1. Conditional effect plot showing associations between Pre-date attractiveness rating and Reaction Time (RT) separate per Gender. The black line represents the median effect, while the grey ribbon represents the 95% credible interval.

Date outcome

Second, we investigated the association between *Date outcome* and *Reaction Time* using a Bayesian mixed model with a Gaussian distribution (Supplementary Table 3; see Appendix G for model stability checks). We found a robust effect of *Date again distractor picture* on *Reaction time*: participants were slower by 4.41 ms to respond to the probe if the distractor image depicted someone they later indicated as a successful date compared to when the distractor image depicted someone that they did not consider a successful date during their speed-dates ($b_{\text{no-yes}} = -4.41$ [1.96], 89% CrI [− 7.51; − 1.29], $pd_- = 0.99$), and this effect did not substantially differ per *Gender* ($b_{\text{women-men}} = -2.48$ [3.93], 89% CrI [− 10.30; 5.26], $pd_- = 0.74$; Figure 2 top panel).

When investigating the effect of *Date again probe picture* on *Reaction Time*, we did not find a robust overall effect ($b_{\text{no-yes}} = 1.68$ [1.94], 89% CrI [− 1.49; 4.70], $pd_+ = 0.81$). However, we did find a robust interaction with *Gender* ($b_{\text{women-men}} = -9.33$ [3.88], 89% CrI [− 16.80; − 1.60], $pd_- = 0.99$). Therefore, we explored the effect of *Date again probe picture* within each level of *Gender.* For women, we found no robust effect ($b_{\text{women}} = -2.97$ [3.06], 89% CrI [− 8.96; 3.12], $pd_- = 0.84$). For men, on the other hand, we found that they responded faster to the probe by 6.33 ms when it replaced a picture of someone whom they later considered a successful date during their speed-dates ($b_{\text{men}} = 6.33$ [2.36], 89% CrI [1.75; 11.00], $pd_+ = 1.00$; Figure 2 lower panel).

Voluntary attention (eye-tracking)

Pre-date attractiveness ratings

We first explored the association between *Pre-date attractiveness rating* and *Looking time bias*, using Bayesian zero–one inflated beta regression (Supplementary Table 4; see Appendix G for model stability checks). We found that attractiveness ratings had a robust effect on voluntary attention. More specifically, participant's attractiveness ratings of the left picture correlated positively with proportion of time spent looking at the left picture ($b = 0.087$ [0.0050], 89% CrI [0.079; 0.095], $pd_+ = 1.00$), while we found the opposite effect for the attractiveness rating of the right picture ($b = -0.098$ [0.0041], 89% CrI [− 0.106; − 0.091], $pd_- = 1.00$). The results were similar for other values of *Pre-date attractiveness rating*: increased attractiveness ratings of the left picture were associated with an increased probability of looking at the left picture, while the opposite was true for the right picture (Supplementary Table 5).

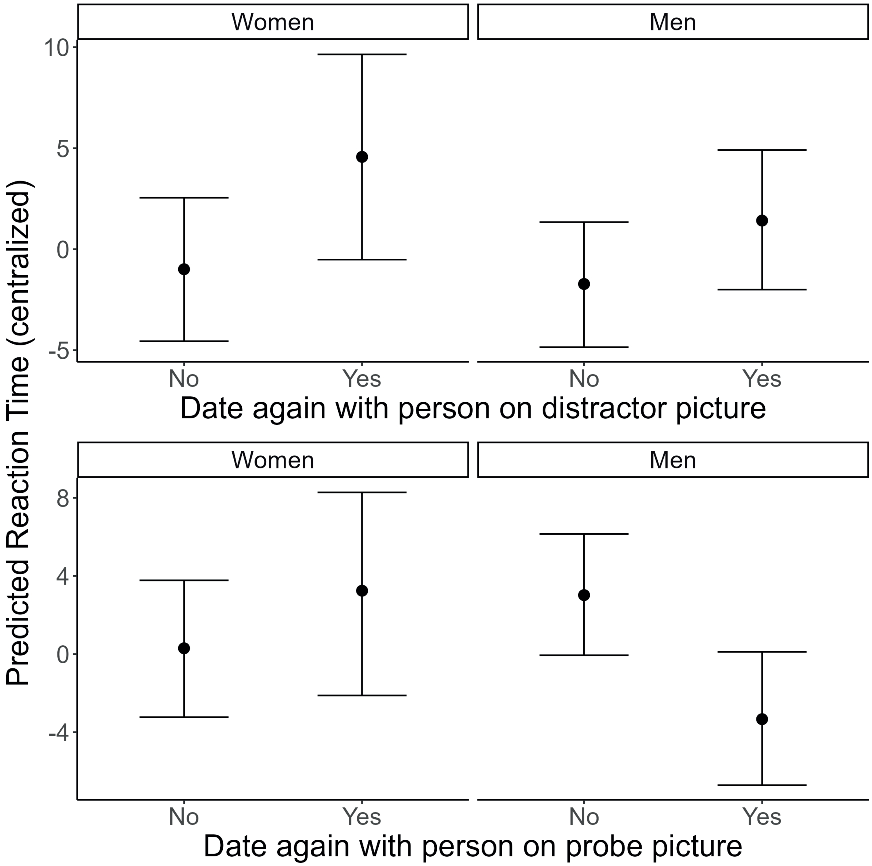

Figure 2. Conditional effect plot showing the effect of Date outcome on Reaction Time (RT) separate per Gender. Values are conditioned on the other predictor set to "No". Error bars represent 95% Credible Intervals.

To see whether the effect was modulated by *Gender*, we compared the slopes for men and women. However, we found no robust interaction between *Gender* and *Pre-date attractiveness rating* for both the left picture ($b_{\text{women-men}} = -0.001$ [0.010], 89% CrI [− 0.026; 0.007], $pd_{-} = 0.83$) and the right picture ($b_{\text{women-men}} = 0.012$ [0.010], 89% CrI [− 0.006; 0.032], $pd_{+} = 0.91$). This pattern was similar for other values of *Pre-date attractiveness rating*: there was no robust difference in slope between men and women (Supplementary Table 6).

We performed the same analysis with the *Post-date attractiveness ratings* as predictor. This analysis yielded the same results (Supplementary Table 7). Altogether, the results show that participants indeed looked longer at faces that they rated as attractive. The results are visualized in Figure 3.

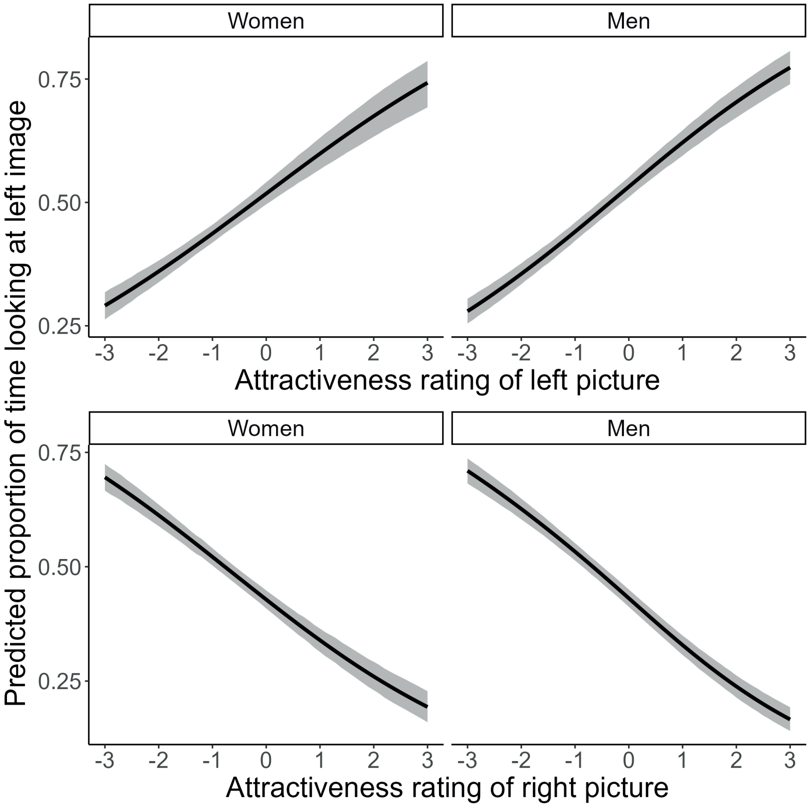

Figure 3. Effect plot showing associations between Pre-date attractiveness rating and Looking time bias separate per Gender. The black line represents the median effect, while the grey ribbon represents the 95% credible interval.

Date outcome

Second, we investigated the association between *Date outcome* and *Looking time bias* using Bayesian zero–one inflated beta regression (Supplementary Table 8; see Appendix G for model stability checks). We found that participants showed more attention towards pictures of people that they later indicated they would like to date again. More specifically, when the left picture depicted someone they wanted to date again, they spent on average 12.4 percentage points longer looking at the left picture than when the left picture depicted someone they did not want to date again ($b_{\text{no-yes}} = -0.124$ [0.019], 89% CrI [− 0.154; − 0.095], $pd_{-} = 1.00$). When the right picture depicted someone they wanted to date again, they spent on average 15.8 percentage points less looking at the left picture than when the right picture depicted someone they did not want to date again ($b_{\text{no-yes}} = 0.158$ [0.017], 89% CrI [0.131; 0.186], $pd_{+} = 1.00$).

To see whether the effect was modulated by *Gender*, we investigated whether the effect for women and men was substantially different. However, we found no consistent gender differences (Left picture: $b_{\text{women-men}}=0.060$ [0.037], 89% CrI [0.002; 0.118], $pd_{+}=0.95$; Right picture: $b_{\text{women-men}}=0.014$ [0.034], 89% CrI [− 0.043; 0.066], $pd_{+}=0.66$), although the *pd* suggested that the effect of *Date outcome* on *Looking time bias* was stronger for men for the left picture specifically.

Altogether, the results show that participants indeed looked longer at the faces of people that they later indicated they wanted to see again after their speed-date (Figure 4).

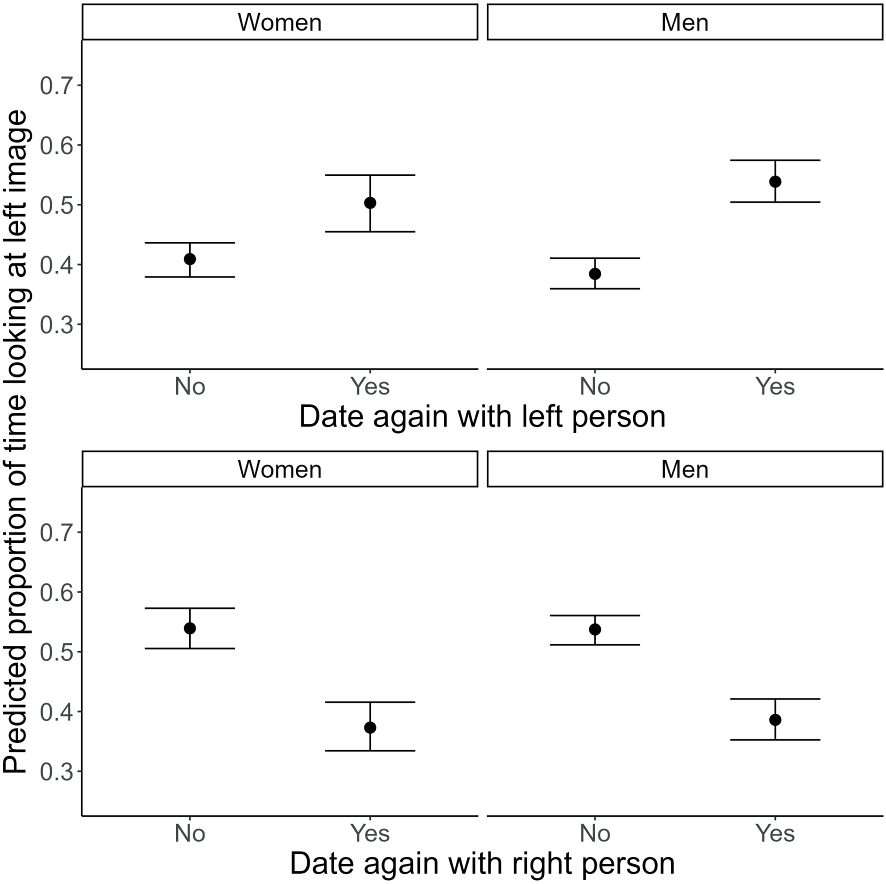

Figure 4. Plot showing the effect of Date outcome on Looking time bias separate per Gender. Error bars represent 95% Credible Intervals.

Model comparisons

Regarding the immediate attention analysis, we found no clear differences in predictive accuracy between the three models (Supplementary Tables 9-11). Although the model that included *Pre-date attractiveness rating* had the highest expected log-predictive density, the differences with the models that included *Post-date attractiveness rating* ($\Delta \text{elpd}_{\text{LOO}} = 10.5$ [9.6]) or *Date outcome* ($\Delta \text{elpd}_{\text{LOO}} = 14.0$ [11.2]) as predictors were not robust due to the relatively high standard errors. Thus, while the model that incorporated *Pre-date attractiveness rating* as predictors had the highest predictive accuracy, there was no substantial difference in predictive accuracy with the two other models.

Regarding the voluntary attention analysis, we found robust differences in predictive accuracy between the three models (Supplementary Tables 12-14). Namely, the model that included *Pre-date attractiveness rating* had a substantially higher predictive accuracy than the models included *Post-date attractiveness rating* ($\Delta \text{elpd}_{\text{LOO}} = 100.1$ [17.4]) or *Date outcome* ($\Delta \text{elpd}_{\text{LOO}} = 133.5$ [17.9]) as predictors. Thus, the model comparisons suggested that pre-date attractiveness ratings might be a better predictor of voluntary attention than post-date attractiveness ratings or date outcome.

Discussion

Here we combined a naturalistic speed-date paradigm with cognitive tasks on attentional biases to investigate how physical attractiveness shaped processes of immediate and voluntary attention, using a dot-probe task and a preferential looking paradigm, respectively. First, consistent with previous literature, we found considerable variation in attractiveness ratings between subjects. With regard to immediate attention, we found that only men's attention was modulated by attractiveness, but we found no consistent association between date outcome and immediate attention. With regard to voluntary attention, we found that both men and women looked longer at faces that they rated as attractive before their date. Furthermore, participants showed more attention towards the faces of people that they later indicated they wanted to date, suggesting that voluntary attention can to some extent reflect mate choice for both men and women. However, model comparisons showed that pre-date attractiveness ratings were more predictive of immediate and voluntary attention than date outcome and post-date attractiveness, although the results are not unequivocal for immediate attention. Below, we discuss these findings and address possible implications and limitations of our study.

Similar to previous work on (dis)agreements in attractiveness ratings, we found an ICC of approximately 0.4 for the pre-date attractiveness ratings (Bronstad & Russell, 2007; Hönekopp, 2006) , reinforcing the idea that individual attractiveness preferences can vary and should be taken into account when studying cognitive aspects of mate choice. Consistent with this idea, we found that individual attractiveness ratings predicted immediate attention in men. This finding extends previous work (Roth et al., 2022) on immediate attention and attractiveness that showed a general attentional bias for faces that were predefined as attractive in a large community sample, but found no effect of sex on this bias. Crucially, this previous study did not account for relationship status. Given that motivation can influence immediate attention (Ma et al., 2019; Ma, Zhao, et al., 2015; Maner, Gailliot, & DeWall, 2007), we only tested non-committed participants who were interested in a relationship, and as mentioned above we used their individual attractiveness ratings as predictor instead of pre-defined categories. Thus, we can conclude that men immediately attended towards faces that they rated as attractive, but we did not find the same result for women. Future research should aim to disentangle and quantify the effects of general attractiveness and individual attractiveness preferences on attention. For example, a recent study on dating behavior (Baxter et al., 2022) showed that both general and individual preferences uniquely contribute to date outcome, but whether this is also the case for attentional processes remains unknown.

It is tempting to interpret our results on immediate attention as evidence for the notion that men are more attuned towards attractiveness than women, which has also been found in previous immediate attention studies (Maner, Gailliot, & DeWall, 2007; Zhang et al., 2017) However, in our exploratory analysis of the interaction between pre-date attractiveness rating and gender, we found a robust gender difference only for the effect of probe picture attractiveness on reaction time. While the effect of distractor picture attractiveness was robust only for men, the difference between men and women itself was not robust. Therefore, we refrain from interpreting the differences between men and women as clear evidence for a sex effect, as previous studies have described the pitfalls of interpreting differences in post-hoc effects as evidence for a robust interaction (Gelman & Stern, 2006; Nieuwenhuis et al., 2011). With regard to the absence of a robust effect in women, in accordance with our findings, previous work has shown that the neural activity of men and women might differ in response to faces varying in attractiveness. Van Hooff et al. (2011) investigated the neural underpinnings of processing attractiveness. They found higher late positive event-related potential (ERP) amplitudes (250–600 ms post cue) in men than women. Crucially, this ERP has been linked to appraisal of facial attractiveness (Werheid et al., 2007). This finding suggests that men might appraise attractiveness differently than women, which could translate into observable differences in processes involving immediate attention (van Hooff et al., 2011). Future research should further investigate the neural underpinnings of appraising attractiveness and how these translate to behavior.

Previous studies on immediate attention and attractiveness heavily relied on consensus attractiveness ratings (Ma et al., 2019; Ma, Zhao, et al., 2015; Maner, Gailliot, & DeWall, 2007; Roth et al., 2022). Here, we examined whether taking the idiosyncratic preferences into account rather than general attractiveness ratings would increase the magnitude of the effect sizes found in the dot-probe task as compared to previous literature. We found that people in general responded 7 ms faster between the least and highest attractiveness rating. However, the difference between the two most extreme conditions (a very unattractive probe picture paired with a very attractive distractor picture, and the other way around) would be ~ 15 ms. This effect size is similar to those that have been typically reported in dot-probe studies (van Rooijen et al., 2017). Regarding the effect of attractiveness on immediate attention, this effect is comparable to a previous study that did not take idiosyncratic preferences into account (Roth et al., 2022). In that study, people had an attentional bias of ~ 9 ms to attractive faces when paired with neutral faces, but had a ~ 6 ms attentional bias to neutral faces when these were paired with unattractive faces. Overall, this indirectly translates to a ~ 15 ms attentional bias to attractive faces compared with unattractive faces. While it is important to note that this is an indirect comparison, and that the methods are slightly different, this effect size fits well with our current finding. In conclusion, contrary to our expectation, taking idiosyncratic preferences into account did not increase the magnitude of previously recorded effects of attractiveness on immediate attention. Instead, the size of the effect of consensus ratings and idiosyncratic ratings on immediate attention seem to be rather similar.

Our hypothesis regarding date outcome and immediate attention were partly supported. Specifically, we found an overall effect of the distractor picture on RT, and an effect of the probe picture for men but not for women. For men, these results are in line with our previously described effects of attractiveness on immediate attention. Given that we found a robust association between attractiveness and immediate attention for men, and that we know that date outcome is strongly associated with attractiveness (Luo & Zhang, 2009; Roth, Samara, & Kret, 2021), it is not surprising that date outcome and immediate attention are associated as well. Of course, physical attractiveness ratings do not perfectly predict date outcome; other processes such as physiological linkage (Prochazkova et al., 2022), nonverbal behavior (Hall & Xing, 2015), attachment styles (Schindler et al., 2010) and perceived similarity (Tidwell et al., 2013) all explain date outcome to some extent as well. Still, the association between attractiveness rating and date outcome might have been strong enough to explain the association between date outcome and RT in the immediate attention task.

In the preferential looking task, we found that both men and women divided their attention based on the attractiveness of the stimuli they were presented with. This is in line with previous work (Leder et al., 2016), but also contrasts with other work that found a gender difference, with men showing a stronger association between voluntary attention and attractiveness than women (Mitrovic et al., 2018). However, it is important to note that participants in our study were all interested in a relationship, i.e., they were motivated to find a partner, while other studies tested both non-committed and committed participants (Mitrovic et al., 2018). As has been suggested, motives can substantially affect cognitive processes (Kenrick et al., 2010). On top of that, participants in our study were aware that they would later meet the people they saw during the tasks, possibly strengthening their motivation even further.

The preferential looking task consisted of trials with a prolonged exposure to the stimuli compared to the dot-probe task. Therefore, participants were able to freely look upon the stimuli and gather more relevant information from the stimuli compared to the dot-probe task. Given that women might need more contextual information in order to appraise a potential partner (Laan & Janssen, 2007), this could possibly also explain why we do not find any sex differences in the preferential looking task, while we do find some evidence for sex differences in the dot-probe task. Future research should further investigate the concordance between immediate and voluntary attention to attractiveness and their relationship to gender.

We also found that date outcome was substantially associated with voluntary attention: participants indicated that they wanted to date again with people that they looked at for longer during the preferential looking task. This again highlights the strong association between attractiveness ratings and initial partner preferences: especially on first dates people seem to employ physical attractiveness as their main selection criterion (Luo & Zhang, 2009; Roth, Samara, & Kret, 2021). Given the strong association between attractiveness rating and voluntary attention, it is not surprising that the association between date outcome and voluntary attention is also robust. An exploratory analysis showed that the associations were not modulated by gender: both men and women showed highly similar trajectories with regard to attractiveness-contingent voluntary attention. Importantly, we consider it unlikely that this effect is driven by uncertainty in the parameter estimates, given that the credible intervals for the interactions between attractiveness rating and gender were very narrow (see Figure 3). Despite the fact that this finding is somewhat inconsistent with evolutionary theories of human mate choice that emphasize sex differences in attractiveness appraisal (Buss & Barnes, 1986; Li & Meltzer, 2015), it is in line with previous speed-dating studies that failed to find gender differences in the appreciation of physical attractiveness (Eastwick & Finkel, 2008; Luo & Zhang, 2009; Roth, Samara, & Kret, 2021). Here, we have extended these findings by showing that both individual attractiveness ratings and date outcome are associated with voluntary visual attention in both men and women. Nonetheless, it should be noted that these analyses were exploratory in nature, and thus no strict inference can be drawn.

One could argue that it is not readily clear whether our findings (both in immediate and voluntary attention tasks) reflect long-term or short-term mate choice dynamics. Previous studies have questioned the ecological validity of speed-date paradigms to capture long-term mate choice processes (Li et al., 2013; Li & Meltzer, 2015). Specifically, Li et al. (2013) argue that speed-date designs might attract people that are not necessarily considering their interaction partners as long-term mates. Thus, they posit that the unique effects of short-term and long-term mate choice cannot be disentangled in speed-date designs, and that it is unclear whether such designs more closely resemble short-term or long-term mate choice contexts. However, it should be noted that almost all of our participants (except for 2) reported that they were interested in pursuing a long-term relationship and, in line with other speed-date events (Asendorpf et al., 2011; Luo & Zhang, 2009), still seemed to value physical attractiveness, although this is often specifically mentioned as a criterium for short-term mates (Li et al., 2013). Furthermore, previous work has shown that long-term partner ratings and physical attractiveness ratings highly correlate (Bressan, 2021; Roth, Samara, & Kret, 2021; Wu et al., 2022). In addition, it remains to be established whether there are specific contexts that emphasize long-term over short-term mate-choice considerations. In fact, a large-scale study showed no evidence that different initial meeting contexts (e.g., bars, church, online) influence divorce rates (Cacioppo et al., 2013). In a speed-date context, it has been shown that first impressions, which are asserted by some to reflect short-term mate choice processes, still predict long-term romantic interest (Baxter et al., 2022). In conclusion, our findings should not be interpreted as the product of uniquely long- or short-term mate choice processes. Instead, our findings would be best interpreted in the context of a close-relationships tradition (Eastwick et al., 2014) that considers short-term and long-term contexts as closely related.

Finally, we attempted to disentangle the effects of attractiveness and date outcome on immediate and voluntary attention by means of Bayesian model comparisons (PSIS-LOO-CV: Vehtari et al., 2017). For immediate attention, these comparisons suggest that pre-date ratings of attractiveness are more predictive of reaction times than date outcome or post-date attractiveness, even though the differences were not robust. Thus, we cannot draw strict conclusions regarding the relative influence of attractiveness and date outcome on immediate attention. For voluntary attention, on the other hand, we found robust evidence in favor of the model that includes pre-date attractiveness ratings over the models that include date outcome and post-date attractiveness rating, respectively. This suggests that voluntary attention is specifically driven by physical attractiveness ratings, which is in line with previous work (Leder et al., 2016; Mitrovic et al., 2016, 2018). Consequently, the robust effect of date outcome on voluntary attention might have been the result of strong intercorrelation between attractiveness ratings and date outcome, as has been reported in many studies (Luo & Zhang, 2009; Roth, Samara, & Kret, 2021). To address this limitation, we suggest that future studies could employ a pre-post-design, where participants engage in attention tasks before and after a speed-date session to study specifically how the experiences gained during the speed-dates alter attentional processes.

Here, we investigated how attractiveness and date outcome were associated with immediate and voluntary attention in non-committed young adults. In line with previous studies, we found substantial inter-individual differences in attractiveness preferences. Furthermore, we found that immediate attention was modulated by attractiveness for men, but not for women, while no consistent relationship between immediate attention and date outcome was found. With regard to voluntary attention, we found that both men and women looked longer at pictures of people that they found attractive and that they wanted to date again. However, attractiveness ratings were more predictive of voluntary attention than date outcome. Our results therefore suggest that especially voluntary attention can provide information about individual preferences and possibly also mate choice of people who are motivated to find a partner.

Chapter 6

No immediate attentional bias towards or choice bias for male secondary sexual characteristics in Bornean orang-utans (*Pongo pygmaeus*)

Abstract

Primate faces provide information about a range of variant and invariant traits, including some that are relevant for mate choice. For example, faces of males may convey information about their health or genetic quality through symmetry or facial masculinity. Because perceiving and processing such information may have bearing on the reproductive success of an individual, cognitive systems are expected to be sensitive to facial cues of mate quality. However, few studies have investigated this topic in non-human primate species. Orang-utans are an ideal model species to test mate-relevant cognitive biases, because they are characterised by male bimaturism: some adult males are fully developed and bear conspicuous flanges on the side of their face, while other males look relatively similar to females. Here, we describe two non-invasive computerised experiments with Bornean orang-utans (*Pongo pygmaeus*), testing (i) immediate attention towards large flanges and symmetrical faces using a dot-probe task (*N* = 3 individuals) and (ii) choice bias for pictures of flanged males over unflanged males using a preference test (*N* = 6 individuals). In contrast to our expectations, we found no immediate attentional bias towards either large flanges or symmetrical faces. In addition, individuals did not show a choice bias for stimuli of flanged males. We did find exploratory evidence for a colour bias and energy efficiency trade-offs in the preference task. We discuss our null results and exploratory results in the context of the evolutionary history of Bornean orang-utans, and provide suggestions for a more biocentric approach to orang-utan cognition.

Based on:

Roth, T. S., Samara, I., Perea-García, J. O., & Kret, M. E. No immediate attentional bias towards or choice bias for male secondary sexual characteristics in Bornean orangutans (*Pongo pygmaeus*). *Manuscript submitted for publication.*

Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/BL87ES

Introduction

Primates have a highly specialized visual system (Barton, 1998; DeCasien & Higham, 2019), and the importance of visual signalling becomes especially apparent in group living species. For example, primates attend to faces of conspecifics (Kano et al., 2012) and discriminate faces based on different characteristics, such as emotional expressions (Pritsch et al., 2017) and familiarity (Leinwand et al., 2022; Lewis, 2017; van Berlo et al., 2023). Importantly, primate faces can also signal cues that are relevant for mate choice, such as health or dominance (Petersen & Higham, 2020). Consequently, primates might have cognitive biases related to sexually relevant facial characteristics. Examples of such traits are sexually dimorphic characteristics and facial symmetry (Little, Jones, et al., 2011; Rhodes, 2006). However, previous work on this topic has mostly focused on rhesus macaques, and very few studies have studied cognitive biases to sexually relevant facial characteristics in great apes. Therefore, the present paper aims to investigate whether Bornean orang-utans (*Pongo pygmaeus*) have cognitive biases for such facial characteristics using an immediate attention task and a preference task.

Cognitive processes are strongly influenced by evolutionarily relevant contexts, such as mate choice (Kenrick et al., 2010; Schaller et al., 2017). Mate choice is one of the most important aspects of an animal's life: choosing a suitable mate might ensure a good representation of the individual's genes in the next generation. Because of this strong incentive to choose a suitable mate, many species have evolved specific mate preferences that guide individuals during the mate choice process (Darwin, 1871; Manson, 2011). For humans, it has been established that preferences affect social cognition: several cognitive processes, such as attention (e.g., Roth et al., 2022, 2023), memory (e.g., Lin et al., 2020), and effort (e.g., Levy et al., 2008), are modulated by physical attractiveness. For non-human primates, research on this topic is still relatively scarce. While previous work has mainly focused on looking preferences, and how these are modulated by sexual dimorphic traits (Dubuc et al., 2016; Rosenfield et al., 2019; Waitt et al., 2003), few studies have investigated other cognitive processes such as direct attention or choice bias (Watson et al., 2012). Furthermore, most of the aforementioned studies have focused on rhesus macaques (*Macaca mulatta*), even though a good understanding of the cognitive processes associated with sexual selection requires investigation of a wide range of species.

Orang-utans are a suitable species to study cognitive biases associated with sexual selection. Unique among mammals, orang-utans are characterised by male bimaturism: while some adult males quickly develop secondary sexual characteristics, such as a throat sac, large body size, and conspicuous flanged on the side of the face, other males experience developmental arrest of these characteristics (Kunz et al., 2022). These so-called unflanged males are sexually mature and can successfully reproduce, although females prefer to mate with fully developed flanged males when they are fertile (Knott et al., 2009). Possibly, female preference for flanged males reflects selection for good genes: the transition from unflanged to flanged male is energetically costly, meaning that males of higher genetic quality would be more likely to develop into flanged males (Knott et al., 2009). Furthermore, fierce male-male competition has been described between flanged males, suggesting that flanged males are also at serious risk of being injured during fights (Knott & Kahlenberg, 2011). Thus, by mating with flanged males, orang-utan females might ensure that their offspring has higher genetic quality. Consequently, it could be beneficial to have cognitive biases to flanged males.

Another trait that is often mentioned with regard to mate choice is facial symmetry, which might reflect the ability to withstand environmental stress during development (Valen, 1962). While clear associations between health and facial symmetry have not been established in humans yet (Pound et al., 2014), previous work on chimpanzees (*Pan troglodytes*: Sefcek & King, 2007) and rhesus macaques (Little et al., 2012) has found that more asymmetrical individuals were also less healthy. In addition, macaques prefer to look at symmetrical faces of conspecifics (Waitt & Little, 2006), which shows that this facial characteristic might modulate attentional processes. Thus, individuals might have cognitive biases for symmetrical conspecifics, because selecting a mate with a symmetrical face could potentially result in more genetically fit offspring.

In this study, we employ two paradigms to investigate immediate attentional bias towards flanged faces and symmetrical faces, and choice bias for flanged faces. In the dot-probe task (MacLeod et al., 1986; van Rooijen et al., 2017), two different stimuli are simultaneously displayed, each one on a different side of the screen. After a set amount of time, both pictures disappear, and a dot appears on the location of one of the pictures. If the dot appears behind the stimulus that the participant was attending to, the participant can quickly indicate the location of the dot by clicking it. However, if the dot appears behind the stimulus that was not receiving the participant's attention, they will first need to switch their attention to the dot before they can indicate the location. Thus, if the dot appears behind a stimulus that immediately attracts attention, participants will be faster to respond than when the dot appears behind a less salient stimulus (van Rooijen et al., 2017). Recently, the dot-probe task has been used to study emotion perception in different primate species (orang-utans: Laméris et al., 2022; chimpanzees: Kret et al., 2018; Wilson & Tomonaga, 2018; rhesus macaques: King et al., 2012; Lacreuse et al., 2013). In addition, the task has successfully been used in humans to study attractiveness bias (Ma et al., 2019; Ma, Zhao, et al., 2015; Roth et al., 2022). In general, these studies have established that individuals immediately attend to evolutionarily relevant stimuli, such as emotional expressions or preferred partners. Therefore, we here employed the dot-probe task to study direct attention towards sexually relevant facial characteristics in orang-utans.

When it comes to choice bias, Watson et al. (2012) developed a paradigm to test choice biases in unrestrained primates. In this task, individuals first learn to associate two coloured dots (red and green) with specific categories (e.g., pictures of faces), so that they can predict what they will see on the screen by clicking a specific dot. During the test phase they can choose between the two coloured dots: both choices yield the same reward, but the picture that will appear on the screen is different. The authors successfully used this method to study preference for sex and status in rhesus macaques: they found that rhesus macaques chose to look more at faces of dominant males and perinea of conspecifics, while they were less likely to choose pictures of low-ranking conspecifics. Because this task has been successfully applied to rhesus macaques, here we used an adapted version to study choice bias for flanges in orang-utans.

The present paper reports the results of two studies. These two studies aimed to investigate direct attentional biases towards flanged and symmetrical faces, and a choice bias for flanged faces in Bornean orang-utans, respectively. Given that the presence of flanges or facial symmetry may be a signal of good genes, we predicted for the dot-probe task that individuals should respond faster on trials where the dot would replace stimuli that depicted males with large flanges or males with symmetrical faces than when the dot replaced stimuli that depicted males with small or no flanges or asymmetrical faces. For the choice task, we expected individuals to more often choose the coloured dot that was associated with pictures of flanged males over the coloured dot that was associated with unflanged males.

Furthermore, for the preference task, we retrospectively decided to explore (i) whether individuals had a colour bias, (ii) whether individuals made choices that might reflect conservation of energy, and (iii) whether individuals showed temporal clustering in their choices. We investigated colour bias because evolutionary theories of colour vision have suggested that the ability to see red co-evolved with frugivory (Bowmaker et al., 1991). With regard to energy conservation, Bornean orang-utans are characterised by extremely low rates of energy use (Pontzer et al., 2010), potentially an adaptation to habitats with long periods of fruit scarcity resulting in negative energy balance (O'Connell et al., 2021; Vogel et al., 2017). Potentially, such energy conservation mechanisms could also influence their responses during the task. Lastly, we also investigated temporal clustering, because flanged males are not only preferred mating partners (Knott et al., 2009), but might also pose a threat (e.g., infanticide: Kunz et al., 2022) or are perceived as threatening (Beaudrot et al., 2009). Consequently, individuals may show temporal clustering in their choices during our task, by either opting for a less arousing picture of an unflanged male after seeing a flanged male stimulus (i.e., more switching, temporal dispersion) or by mostly sampling flanged male stimuli, until arousal reaches a certain threshold and individuals switch to unflanged stimuli instead (i.e., fewer switches, temporal clustering). Thus, because of socio-ecological characteristics, we decided to explore these three topics in addition to our main questions.

Methods

Subjects and housing

The animals that participated in this study were part of a population of 9 Bornean orang-utans (*Pongo pygmaeus*) at Apenheul Primate Park, The Netherlands (Table 1). They were kept in a fission-fusion housing system consisting of 4 enclosures, meaning that they were in small subgroups with changing composition over time, in order to mimic the natural social system of the species. Some individuals never shared enclosures to avoid conflict (e.g., the two adult males). Each enclosure consisted of an inside part and an outside part. The orang-utans were fed multiple times a day, and had ad libitum access to water. Most of the orang-utans had previously been exposed to touchscreens for a previous dot-probe study (Laméris et al., 2022), but only two of the orang-utans from that previous study (Sandy & Samboja) eventually participated in this study.

With regard to participation in the experiments described here, three individuals participated in the dot-probe experiments (both flange size and symmetry version), while six individuals participated in the preference test. Table 1 indicated which individuals participated in the experiments.

Table 1 – Orang-utans housed in Apenheul at the time of study.

Name	Sex	Date of birth	Origin	Dot-probe	Preference test
Kevin	M	~1982	Wild		
Sandy	F	29-4-1982	Captive	Yes	Yes
Wattana	F	17-11-1995	Captive		Yes
Amos	M	20-12-2000	Captive		
Samboja	F	9-6-2005	Captive	Yes	Yes
Kawan	M	22-2-2010	Captive	Yes	Yes
Baju	M	2-12-2015	Captive		Yes
Indah	F	19-10-2017	Captive		Yes

Apparatus

Touchscreen experiments were conducted via E-Prime 2.0 on a TFT-19-OF1 Infrared touchscreen (19”, 1280 x 1024 pixels). The touchscreen setup was encased in a custom-made setup which was incorporated in one of the orang-utans’ night enclosures. This night enclosure could be made accessible from two of the main enclosures by the animal caretakers. The researchers controlled the sessions on a desktop computer connected to the touchscreen setup and could keep track of the orangutans’ responses on the touchscreen through a monitor that duplicated the touchscreen view. Additionally, the researchers had access to a livestream with a camera that was built in the enclosure, allowing them to observe the participant. Correct responses were rewarded with a sunflower seed on a 100% fixed reinforcement ratio. For most individuals, the rewards were delivered by a custom-built autofeeder linked to the desktop computer, that dropped a reward in a PVC chute. However, Kawan and Baju did not habituate properly to the presence of the feeder, and kept trying to push it over with sticks. Therefore, we decided to reward them manually. The researcher was positioned behind the setup which prevented visual contact between the orangutans and researchers.

Stimuli

Dot-probe task

For dot-probe task with flange size manipulation, we collected 72 images depicting front-facing Bornean or Sumatran orang-utan males with flanges. The images were collected through image hosting websites and social media groups. We edited the stimuli in GIMP (v2.10.32). First, we cropped the faces. Second, we consecutively selected the flanges on the left and right side of the face, respectively. We defined the width of the flange as the distance between the horizontally most peripheral point of the face and the most peripheral point of either the eye region or beard. Hereafter, we increased the width of the flanges (measured in pixels) with 15 percent to obtain the stimulus with enlarged flanges, and we decreased the width with 15 percent to obtain the stimulus with reduced flanges. We chose 15 percent to make sure that the stimuli would not become abnormal in terms of flange size. In total, this resulted in 72 combinations of enlarged and reduced stimuli.

Using the same 72 images, we created the stimulus set for the dot-probe with symmetry manipulation Here, we could only include the images where the faces of the orang-utans appeared to be nearly exactly frontally facing. To determine this, we visually expected whether the eyes and nostrils were at a similar distance from the vertical midline of the face and whether they were of approximately similar size. This was the case for 49 of the images. Next, we created symmetrical versions of the face by mirroring either the left or the right hemisphere at the vertical midline of the face. Thus, from every stimulus, we obtained two symmetrized versions: one based on the left hemisphere and one based on the right hemisphere. Importantly, in some stimuli we employed an extra step to remove squinting that resulted from the mirroring. To this effect, we selected one of the eyes, and mirrored it, resulting in more congruent gaze direction of the eyes. Furthermore, some of the mirrored stimuli were characterised by abnormal facial shape, which is a well-known issue in symmetrized stimuli (Rhodes, 2006). If this was the case, we excluded the stimulus. In total, we obtained 80 stimulus pairs consisting of one symmetrized face and the original face showing natural variation in symmetry.

Preference task

For the preference task, we used 104 stimuli (52 flanged, 52 unflanged) of Bornean orang-utans. The stimuli were collected from the Internet, mainly from release reports published by Bornean orang-utan reintroduction programs. These were supplemented with portrait pictures taken from semi-wild orang-utans and pictures of zoo-housed orang-utans within the orang-utan EEP. All of the stimuli depict front-facing Bornean orang-utan males. We cropped their faces using GIMP (v2.10.32) and pasted the cropped faces on a light-grey background (#808080), resulting in stimuli with an 18:13 aspect ratio. From both the flanged and the unflanged stimuli, we randomly selected four stimuli (eight in total) to use as stimuli in the forced-trial phase of the experiment. The remaining 48 stimuli of each category were randomly distributed across three sessions.

Procedure

Dot-probe task

The procedure for the dot-probe task was almost identical to the one described in Laméris et al. (2022). A trial consisted of five phases (Figure 1). First, a 200x200-pixel black dot appeared on a random position on the screen and had to be clicked. We added this step to avoid anticipatory responses. Second, the dot appeared in the lower, middle part of the screen. Touching this dot activated presentation of two stimuli (500x375 px) that were vertically positioned in the middle of the screen, and horizontally equidistant from the center of the screen (20% vs. 80%). After 300ms, the stimuli disappeared and only one of the stimuli was replaced by a dot (the probe) that remained on the screen until touched by the subject. Touching the dot resulted in a reward (sunflower seed). After an inter-trial interval of 3s, a new trial started. The background of screen was white during all steps of the trial.

Trials were presented in randomized order. For the flange size dot-probe, each individual participated in 6 sessions consisting of 24 trials. For the symmetry dot-probe, each individual participated in 8 sessions consisting of 20 trials. All stimuli were presented twice across all sessions: once as probed stimulus (replaced by dot), once as distractor stimulus (not replaced by dot). At the end of the test sessions, we created extra sessions per subject to repeat outlier trials (see Statistical analysis). All data were collected between February and December 2020, with a test stop between March and July 2020 due to COVID-19.

Two of the three participating individuals were already trained on the task for a previous study (Laméris et al., 2022). They received a few training sessions to check whether they still executed the task correctly, which was the case. For the other individuals, we employed a similar training procedure. Only one of the individuals, Kawan, managed to pass all phases of the training (between July and December 2019). Thus, this resulted in a total sample of three participants.

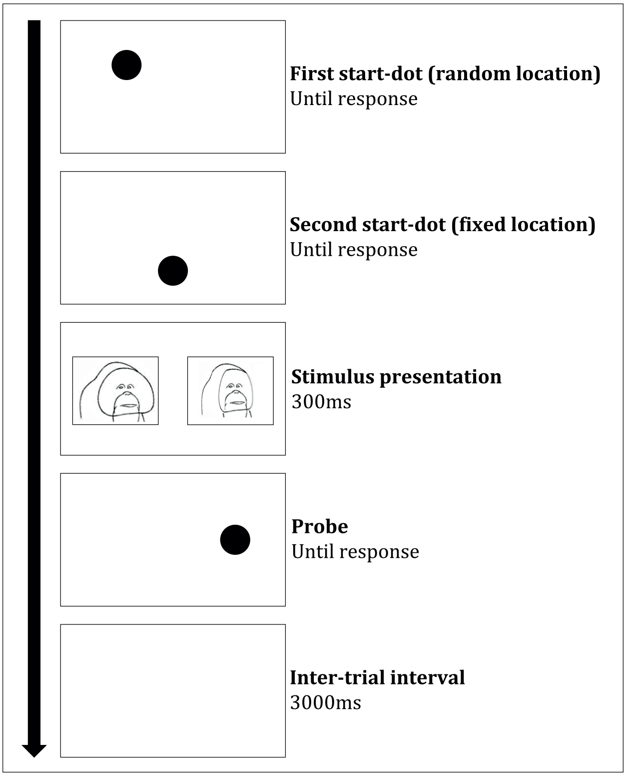

Figure 1 – Schematic depiction of a dot-probe task trial with large and small flanges as competing stimuli. The arrow indicates the temporal progression of the trial.

Preference task

The procedure of the preference task was adapted from Watson et al. (2012). Each session consisted of two parts (Figure 2): a forced-trial procedure (8 trials) and a choice-trial procedure (16 trials). During all parts of the experiment, the background was silver gray (#c0c0c0). Trials in the forced-trial procedure started with a 300x300-pixel black dot that appeared in a random position. This randomly located dot was added at the start of each trial to avoid anticipatory responses. After clicking the dot, a similar dot appeared exactly in the center of the screen. By clicking this dot, individuals would advance to a screen that depicted either a red dot or a green dot. The shades of green (#339900) and red (#990000) were almost equal in saturation. Each dot colour was associated with one specific stimulus category within the session (either flanged or unflanged stimuli). Because there was only one dot on the screen (either green or red), they were “forced” to select this one. After their response, they would be presented with a stimulus from the corresponding category for 4s (820x1134 px) and receive a reward, followed by a 2s inter-trial interval. In total, subjects had to pass 8 forced trials (4 green, 4 red) at the start of each session, in order to probe the association between dot colour and stimulus category within the session.

Hereafter, they were presented with 16 choice trials. The start and end of each choice trial were essentially the same as for the forced trials. However, instead of being presented with *one* coloured dot, subjects could now choose between the red dot and the green dot, thereby controlling the stimulus category on the screen. The dots were presented in a circular way, equidistant from the center of the screen and always located exactly opposite of each other. Note that this differs from the method that Watson et al. (2012) describe, who presented the choice dots always at the same location on the screen. However, we noticed during the familiarisation sessions that the orang-utans would show anticipatory responses because they would know the exact location where the dots would appear. Therefore, we chose to randomize the location of the choice dots in a circular way. Importantly, the coloured dots were always located at the same distance from the center of the screen, where subjects needed to tap to advance to the choice dots.

With regard to training, all individuals were already familiar with clicking dots for a reward. Therefore, we mainly had to familiarise them with the specific task (between July and October 2021). To this effect, all participating subjects fulfilled eight sessions. The first six sessions presented them with pictures of animals and flowers. Importantly, in these sessions we had not yet implemented the randomized location of the choice dots. They were presented on fixed locations, as in the original method (Watson et al., 2012). Because we noticed that individuals would sometimes anticipate the appearance of the choice dots by clicking their location repeatedly before onset, we decided to run two final sessions in which we implemented the randomised circular presentation described above. Subjects could only participate in the experimental sessions after participating in all eight of the familiarisation sessions. In total, six subjects fulfilled this criterion: all individuals except for the two flanged males.

In total, each subject participated in six experimental sessions between September and December 2021, depending on whether the subject already finished the familiarisation phase. In three of the sessions, flanged stimuli were associated with red dots, and in the three other sessions, flanged stimuli were associated with green dots. Subjects were presented with the sessions in blocks based on the colour-stimulus category association, so that they did not have to re-learn the association *each* session. The order of the blocks was randomized between subjects, so that three individuals first received the sessions in which the red dot was associated with the flanged stimuli and three individuals first received the sessions in which the green dot was associated with the flanged stimuli. Within blocks, the order of sessions was randomized.

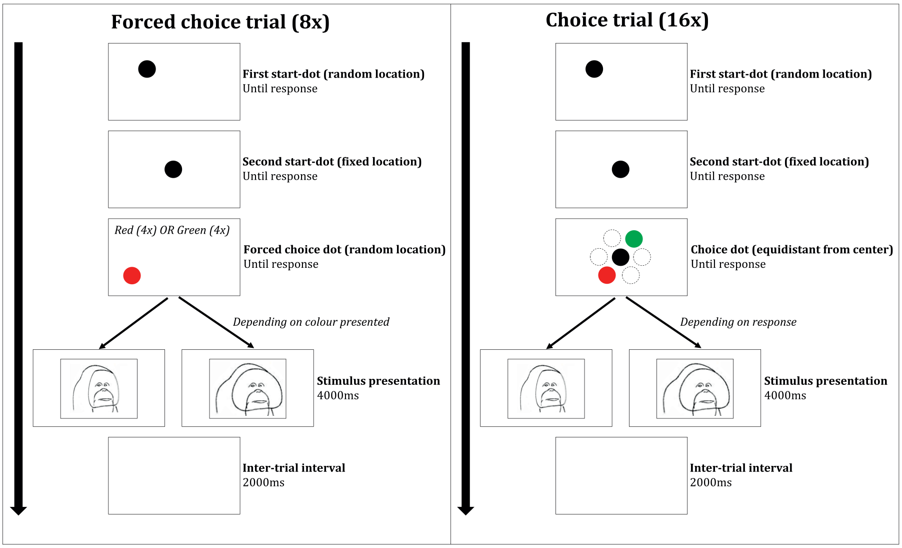

Figure 2 – Schematic depiction of two preference task trials with flanged and unflanged stimuli. The left box shows the design of a forced choice trial, while the right box shows the design of a choice trial. The arrows indicates the temporal progression of the trial.

Statistical analysis

We performed all of the analyses in R statistics Version 4.2.2. To analyse the data, we used Bayesian mixed models. Bayesian analyses have gained in popularity over the past few years because they have a number of benefits compared to frequentist analyses (Kruschke et al., 2012; Makowski et al., 2019). While frequentist methods (e.g., p-value null-hypothesis testing: Wagenmakers, 2007) inform us about the credibility of the data given a hypothesis, Bayesian methods inform us about the credibility of our parameter values given the data that we observed.

This is reflected in the different interpretation of frequentist and Bayesian confidence intervals: The first is a range of values that contains the estimate in the long run, while the latter tells which parameter values are most credible based on the data (Kruschke et al., 2012; McElreath, 2018). Furthermore, Bayesian methods allow for the inclusion of prior expectations in the model, are less prone to Type I errors, and are more robust in small and noisy samples (Makowski et al., 2019). Altogether, these reasons make Bayesian methods a useful tool for data analysis.

All models were created in the Stan computational framework and accessed using the brms package (Bürkner, 2017, 2018), version 2.18.5. All models were run with 4 chains and 6000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van de Schoot, 2017). We found no divergences or excessive autocorrelation in any model. Furthermore we used the package emmeans (Lenth, 2023) to obtain posterior draws for contrasts. Below, we discuss the specific statistical models for each experiment.

Dot-probe task

In line with previous studies (Lacreuse et al., 2013; Laméris et al., 2022; Leinwand et al., 2022; van Berlo et al., 2023) we filtered the reaction times (RTs). First, we excluded slow reaction times, because they might reflect low motivation or distraction. Instead of opting for a fixed outlier criterion (e.g., Leinwand et al., 2022), we determined the upper limit per subject based on the median absolute deviation (MAD) in RT (i.e., RT = median + 2.5 × MAD; Leys et al., 2013). Second, we excluded reactions times <200ms, because they very likely represent anticipatory responses (Whelan, 2008). After the repetition of these unsuccessful trials, we applied the same filtering criteria.

For the flange size dot-probe, we collected 423 trials of which 96 were excluded based on the outlier criteria (22.69%). In the repetition sessions, we collected 105 trials, 28 of which were excluded based on the outlier criteria (26.67%). Thus, our final dataset for the flange size dot-probe contained 404 trials (Kawan: 133; Samboja: 131; Sandy: 140). For the symmetry dot-probe, we followed the same procedure. In total, we collected 474 trials, 102 of which were excluded based on the outlier criteria (21.61%). In the repetition sessions, we collected 108 trials, 32 of which were excluded (29.63%). Thus, our final dataset for the symmetry dot-probe contained 448 trials (Kawan: 152; Samboja: 142; Sandy: 154).

For both experiments, we created separate statistical models per subject. We chose to analyze our data at the individual level because of the low number of subjects that participated in this experiment. Given the fact that we had a relatively high number of trials per subject, it was possible to test for the presence of a within-subject effect separately for each subject. Previous work has suggested that this is a suitable approach in case of low subject numbers (Craig & Abramson, 2018; Farrar et al., 2020).

To test whether the orang-utans had an attentional bias for large flanges, we fitted three Bayesian mixed models with a Student-*t* family. The Student-*t* family is ideal for robust linear models, as the model will be influenced less strongly by outliers. We specified mean-centered RT (in ms) as dependent variable, and Congruence (Congruent: probe behind large flange stimulus; Incongruent: probe behind small flange stimulus) as categorical independent variable. We added Probe location (Left/Right) as categorical independent variable to control for possible side biases in RT. Furthermore, we allowed the intercept to vary by Session, so that the statistical model accounted for variation in RT between sessions. We specified a Gaussian prior with $M = 0$ and $SD = 5$ for the Intercept of the model. For the independent variables, we specified regularizing Gaussian priors with $M = 0$ and $SD = 10$. For the *nu* parameter of the Student-*t* distribution, we specified a Gamma prior with $k = 2$ and $\theta = 0.1$. For all variance parameters, we kept the default half Student's t priors with 3 degrees of freedom. To test whether orang-utans had an attentional bias for symmetrical faces, we followed the exact same procedure. However, the predictor Congruence now refers to the symmetry of the depicted face (Congruent: probe behind symmetrical stimulus; Incongruent: probe behind original stimulus). We used sum-to-zero coding for all of our categorical independent variables.

Preference task

For 5 of the 6 subjects we had a complete dataset of 96 choice trials. Only for Kawan we missed 4 trials, because he left twice at the end of an experimental session. Thus, our final dataset consisted of 572 datapoints. Because we had a larger number of subjects in this experiment, we chose to analyze the data in one statistical model. To examine whether the orang-utans preferred seeing a picture of flanged males over unflanged males, we fitted a Bayesian logistic mixed model (Bernoulli family). We specified the binary choice (1 = flanged, 0 = unflanged) as dependent variable. The within-subject categorical variable Colour Flanged, which represent whether the flanged stimuli were associated with the red or the green dot, was added as an independent variable, together with the between-subject variable Order, which represented whether the individual first received the sessions in which the red dot was associated with the flanged stimuli or in which the green dot was associated with the flanged stimuli. To explore the effect of dot location on the screen on probability of selection, we extended the model by adding a continuous predictor that was zero-centered and reflected the location of the dot representing flanged stimuli relative to the vertical middle of the screen (range -0.35 – 0.35, with negative values representing the higher portion of the screen).

With regard to the random effects, we allowed the intercept to vary by Subject and allowed the intercept of Session to vary within Subject. Furthermore, we allowed the slope for Colour Flanged to vary by Subject, to take into account potential treatment effects between subjects. We specified a Gaussian prior with $M = 0$ and $SD = 0.5$ for the Intercept and independent variables of the model. Note that these priors are specified on the logit scale. For all variance parameters, we kept the default half Student-*t* priors with 3 degrees of freedom.

To explore temporal clustering and dispersion in the choices of the orang-utans, we developed an R script based on (Gelman et al., 2004, p. 163) that is essentially a Beta-Binomial model that can be used to assess independence of binary observations. We applied it to each of the sessions independently. The script first counts the number of switches between selected categories within the session (variable T). Second, we specified a Beta(10, 10) prior on θ, the probability of selecting a flanged male stimulus, emphasizing a relatively strong expectation of 50/50 selection of flanged and unflanged stimuli. Third, we obtained a posterior for θ by updating the Beta(10, 10) prior based on the choices from the session. Fourth, we simulated 10,000 binary series of the same length as the session, based on sampling from the posterior distribution of θ. Note that the binary series consisted of independent samples. Fifth, based on these simulations, we counted the number of switches T in each independent series, and obtained a distribution of T under the assumption of independence. This allowed us to compare the observed T within the sessions with the expected T under the assumption of independence. Consecutively, we checked whether the observed T fell outside of the 95% Highest Density Interval of the expected T, and we calculated the proportion of expected T-samples that was either similar or higher, or similar or lower than the observed T. With regard to the interpretation, an observed T that is low compared to the distribution of expected T reflects fewer switches in a session than expected under the assumption of independence, hence temporal clustering of choices. An observed *T* that is high compared to the distribution of expected *T* reflects more switches in a session than expected under the assumption of independence, hence temporal dispersion of choices.

Effect size indices

The effect size indices that we report are based on the posterior distributions of each statistical model. We report multiple quantitative measures to describe the effects. First, we report the median estimate (*b* or *OR*), and median absolute deviation of the estimate between square brackets. Second, we report an 89% highest density interval of the estimate (89% CrI). We have chosen 89% instead of the conventional 95% to reduce the likelihood that the credible intervals are interpreted as strict hypothesis tests (McElreath, 2018). Instead, the main goal of the credible intervals is to communicate the shape of the posterior distributions. Third, we report the probability of direction (*pd*), i.e., the probability of a parameter being strictly positive or negative, which varies between 50% and 100% (Makowski et al., 2019).

Ethics

This study employed only non-invasive methods and animals were never harmed or punished in any way during the study. Participation was completely voluntary, animals were tested in a social setting, and animals were never deprived of food or water. The care and housing of the orangutans was adherent to the guidelines of the EAZA Ex-situ Program (EEP). Furthermore, our research complied with the ASAB guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2023), was carried out in accordance with the national regulations, and was approved by the zoological management of Apenheul Primate Park (Apeldoorn, The Netherlands).

Results

Dot-probe

Flange size

In the flange size dot-probe, we found no attentional bias for larger flanges in any of the three participating orang-utans (Figure 3A; Supplementary Table 1; see Appendix G for model stability checks); whether the probe replaced the large or small flange picture had no robust effect on the RT of Kawan ($b_{congruent}$ = -3.28 [8.50], 89% CrI [-16.66; 10.49], *pd* = 0.65), Samboja ($b_{congruent}$ = 3.90 [9.38], 89% CrI [-10.68; 19.25], *pd* = 0.66), and Sandy ($b_{congruent}$ = 2.08 [9.13], 89% CrI [-13.05; 16.52], *pd* = 0.59). We also found no robust effect of probe location (left/right) on RT, indicating that Kawan (b_{left} = 5.08 [8.66], 89% CrI [-9.05; 18.41], *pd* = 0.72), Samboja (b_{left} = -6.61 [9.41], 89% CrI [-21.82; 8.60], *pd* = 0.76), and Sandy (b_{left} = 7.58 [9.30], 89% CrI [-7.33; 22.12], *pd* = 0.80) did not have a side bias.

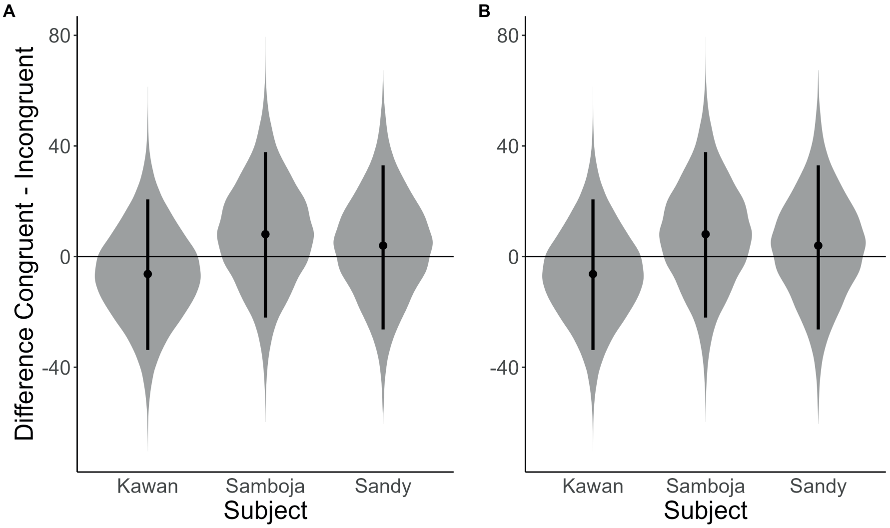

Figure 3 – Posterior predictions of the difference in RT between trials where the probe replaced (A) the stimulus with larger flanges (Congruent) and trials where the probe replaced the stimulus with smaller flanges (Incongruent), or (B) replaced the stimulus with symmetrized face (Congruent) and trials where the probe replaced the stimulus with original face (Incongruent). Values under the horizontal null-line mean that the subject was predicted to respond faster to congruent than incongruent trials.

Symmetry

In the symmetry dot-probe, we found no attentional bias for symmetrical faces in any of the three participating orang-utans (Figure 3B; Supplementary Table 2; see Appendix G for model stability checks); whether the probe replaced the large or small flange picture had no robust effect on the RT of Kawan ($b_{congruent}$ = -3.28 [8.50], 89% CrI [-16.66; 10.49], *pd* = 0.65), Samboja ($b_{congruent}$ = 3.90 [9.38], 89% CrI [-10.68; 19.25], *pd* = 0.66), and Sandy ($b_{congruent}$ = 2.08 [9.13], 89% CrI [-13.05; 16.52], *pd* = 0.59). Similar to the flange size experiment, we found no robust effect of probe location (left/right) on RT, indicating that Kawan (b_{left} = 5.08 [8.66], 89% CrI [-9.05; 18.41], *pd* = 0.72), Samboja (b_{left} = -6.61 [9.41], 89% CrI [-21.82; 8.60], *pd* = 0.76), and Sandy (b_{left} = 7.58 [9.30], 89% CrI [-7.33; 22.12], *pd* = 0.80) did not have a side bias.

Preference task

In the preference test (Supplementary Table 3; see Appendix G for model stability checks), we found that the orang-utans chose stimuli of flanged and unflanged males exactly at chance level ($OR_{Intercept}$ = 1.00 [0.13], 89%CrI [0.78; 1.25], *pd* = 0.52). Thus, they did not seem to prefer looking at stimuli of flanged males. This was the case for all individuals (Figure 4): Baju ($OR_{Intercept}$ = 1.13 [0.30], 89%CrI [0.66; 1.61], *pd* = 0.67), Indah ($OR_{Intercept}$ = 0.85 [0.24]], 89%CrI [0.51; 1.27], *pd* = 0.72), Kawan ($OR_{Intercept}$ = 1.07 [0.26], 89%CrI [0.68; 1.56], *pd* = 0.61), Samboja ($OR_{Intercept}$ = 0.93 [0.23], 89%CrI [0.57; 1.31], *pd* = 0.55), Sandy ($OR_{Intercept}$ = 1.06 [0.25], 89%CrI [0.66; 1.54], *pd* = 0.59), and Wattana ($OR_{Intercept}$ = 1.00 [0.13], 89%CrI [0.78; 1.25], *pd* = 0.52).

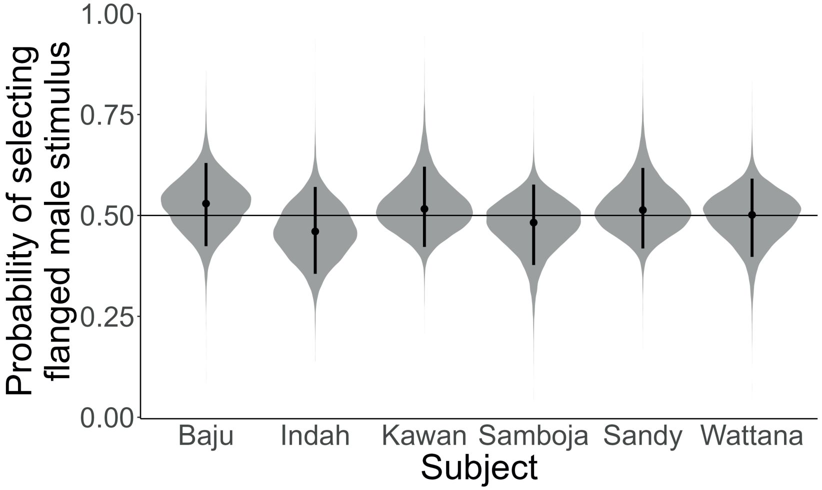

Figure 4 – Posterior predictions of the probability of selecting the flanged male stimulus per subject. The horizontal line indicates chance level.

The between-subject effect of Order did not have a robust effect on the preference of the individuals ($OR_{FlangedRedFirst}$ = 0.88 [0.11], 89%CrI [0.69; 1.07], *pd* = 0.84). However, the colour of the dot that was associated with flanged males did have an influence on the preference: the orang-utans were more likely to select the flanged male stimulus if these were associated with the red dot (OR_{Green} = 0.67 [0.08], 89%CrI [0.54; 0.83], *pd* = 0.99), indicating a preference for the colour red (Figure 5). Furthermore, we found very strong evidence for the notion that orang-utans made energy-efficient choices (Supplementary Table 4; Figure 6): they were more likely to select the flanged stimulus when the dot associated with it was presented in the lower portion of the screen (OR_{Height} = 17.01 [5.06], 89%CrI [9.42; 25.64], *pd* = 1.00).

In addition, we explored whether individuals showed temporal clustering in their choices by selecting the same category multiple times in a row. To this effect, we compared the number of switches between categories for every session to a dataset consisting of the number of switches that one would expect under the assumption of independence. We found no evidence for temporal clustering (fewer switches than expected) or temporal dispersal (more switches than expected) in any of the sessions, indicating that previous choices did not influence choices in the next trial.

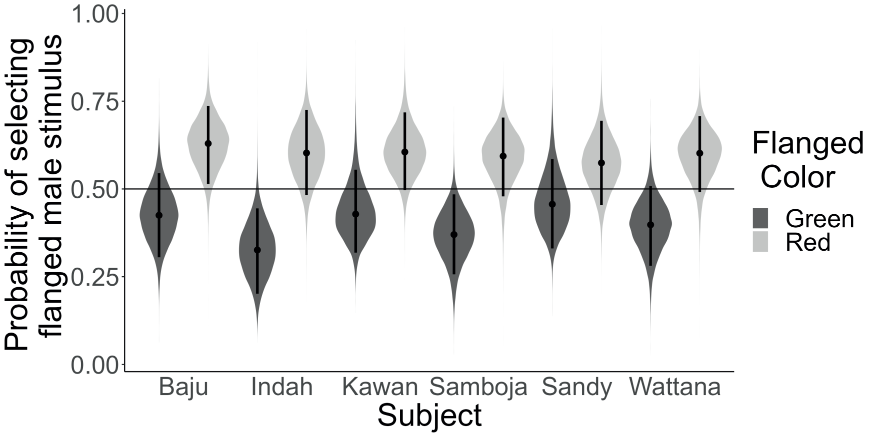

Figure 5 – Posterior predictions of the probability of selecting the flanged male stimulus as a function of the colour associated with flanged male stimuli per subject. The horizontal line indicates chance level.

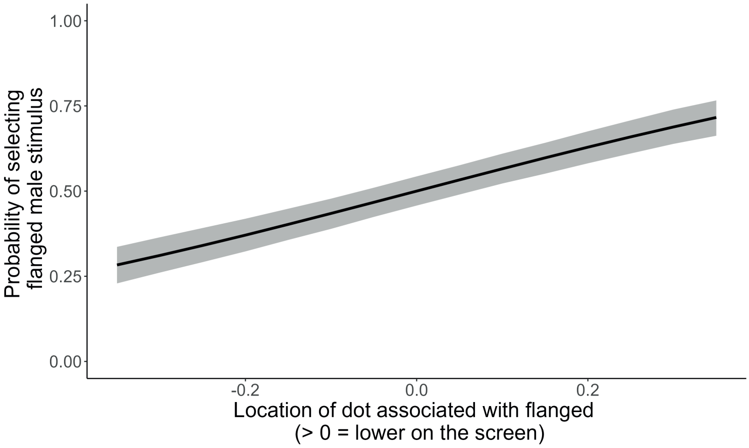

Figure 6 – Posterior predictions of the probability of selecting the flanged male stimulus as a function of the vertical position of the dot representing the flanged male on the screen. Negative values indicate that the dot associated with the flanged male stimulus was positioned in the higher portion on the screen, while positive values indicate the lower portion of the screen.

Discussion

Even though face perception in primates has been studied extensively, the interplay between facial traits relevant to mate choice and cognition has received relatively little attention, especially in great apes. Therefore, the aim of this study was to investigate whether zoo-housed Bornean orang-utans (*Pongo pygmaeus*) have cognitive biases for males with fully developed secondary sexual traits (flanged males) or males with more symmetrical faces. Across two experiments, measuring either immediate attention bias or choice bias, we found no evidence of cognitive biases towards facial traits that might be relevant for mate choice. This lack of biases was consistent between all participating individuals. Furthermore, we did not find evidence for either temporal clustering or dispersion in the preference test: orang-utans did not seem to alter their choices based on their response in previous trials. However, we did find evidence of (i) a robust colour bias and (ii) an energy conservation strategy in the preference test. Below, we discuss our results in the context of primate literature and orang-utan ecology, and consider methodological limitations.

Contrary to our hypotheses, we found no evidence for immediate attentional biases towards either large flanges or symmetrical faces in the dot-probe paradigm, while we expected a bias towards larger flanges and more symmetrical faces. With regard to flanges, previous research has shown that orang-utans spend a substantial amount of time looking at flanges while scanning male faces (Kano et al., 2012). However, it is possible that the manipulation we used, which involved presenting faces with slightly larger or smaller flanges, did not generate salient enough differences between the stimuli to produce robust variations in reaction times. Therefore, future research could repeat the approach with different combinations of flanged and unflanged males instead. Regarding symmetry, we recently reported a similar null result in humans in the exact same task (Roth et al., 2022): human participants had no attentional bias towards symmetrical faces. While the aforementioned explanation of too little difference in salience between stimuli would also apply to our null results in the current study, there is also an important theoretical consideration. While previous literature has often emphasised the importance of symmetry for mate choice (Gangestad et al., 1994; Møller & Thornhill, 1998), recent literature has criticised this notion in humans on the basis that the link between symmetry and attractiveness seems overstated (Jones & Jaeger, 2019)and the link between symmetry and health remains equivocal (Pound et al., 2014). Thus, while our null findings could be the result of methodological limitations, the results for facial symmetry are in accordance with recent null findings and theoretical debates in humans.

Moreover, the experimental paradigm that we used to study immediate attention, the dot-probe paradigm, has been subject to debate in humans due to its relatively poor reliability (Kappenman et al., 2014; Rodebaugh et al., 2016). Similarly, some inconsistent results have been observed when applying this paradigm to primates. While the paradigm has successfully shed light on the influence of emotion information on cognition in various primate species (King et al., 2012; Kret et al., 2016; Lacreuse et al., 2013; Schino et al., 2020; van Berlo et al., 2023), inconsistencies persist. For example, we have recently shown that Bornean orang-utans do not seem to show the expected attentional bias towards emotions in the dot-probe task (Laméris et al., 2022). This raises the question of whether such a widely reported bias is genuinely absent in Bornean orang-utans or if the current paradigm fails to capture it adequately. One potential methodological reason for these inconsistencies is that the dot-probe paradigm relies on reaction times, which are inherently noisy (Morís Fernández & Vadillo, 2020). Especially for species with relatively low levels of manual dexterity compared to humans, such as orang-utans (Bardo et al., 2017), reaction time might not be the most suitable dependent measure in cognitive tasks. Instead, more fine-scaled methods such as non-invasive eye-tracking could be considered to study attentional preferences in primates. These methods are relatively easy to implement in primates (Hopper et al., 2021), and provide a more direct measure of attention (Armstrong & Olatunji, 2012). Correspondingly, we did find an immediate attention bias towards flanged males in an eye-tracking task (see Chapter 7). This suggest that eye-tracking allows us to probe cognitive biases that are potentially too subtle to identify using reaction time tasks, at least in orang-utans.

In the preference task, we used a previously developed paradigm (Watson et al., 2012) to test whether Bornean orang-utans would choose to be presented with flanged or unflanged stimuli. However, all individuals selected flanged and unflanged stimuli equally often. Our results are in contrast with the results that Watson et al. (2012) found in rhesus macaques, who specifically selected stimuli depicting faces of high-ranking individuals or stimuli showing coloured perinea. While we made some minor adaptations to the original paradigm (longer stimulus presentation, no fixed dot locations to avoid anticipatory responses, no indirect comparison of stimulus categories), we do not consider it likely that these changes explain the null results. One potential explanation relies on the fact that both of the choices were rewarded equally, meaning that there was no incentive to choose one category over the other in principle. Because Bornean orang-utans are often confronted with long periods of fruit scarcity (Vogel et al., 2017), they might be especially sensitive to food reward. Potentially, the anticipation of reward during the trial was so salient for them that the means to get to the reward became relatively unimportant. This raises the question whether extrinsically rewarded touchscreen experiments like the one we used here are suitable to study Bornean orang-utan cognition.

We also found that individuals had a higher tendency to choose the flanged male stimulus when it was associated with a red-coloured dot instead of the green-coloured dot, despite the fact that the dots were similar in saturation. This preference for red may indicate a general sensory bias towards the colour red, which could be attributed to the evolutionary pressure on primates to select ripe fruits or young leaves (Fernandez & Morris, 2007). This bias for red objects might extend beyond fruits, possibly explaining why the individuals in the study were more likely to select the red dot. However, previous reports present conflicting evidence regarding the colour bias in food preferences among orangutans. While one report suggested a preference for red food in a juvenile orang-utan (Barbiers, 1985), a more recent report did not find any colour bias (Sauciuc et al., 2016). It is important to note that both reports concern single-subject observations. A more comprehensive study in rhesus macaques demonstrated a bias towards red food items, but this bias did not extend to non-food objects (Skalníková et al., 2020). In conclusion, we found evidence for the notion that orang-utans have a sensory bias towards red objects, although this seems to conflict somewhat with existing literature on colour biases in primates.

In addition, orang-utans were more likely to select the dot associated with flanged male stimuli if it was in the lower portion of the screen, potentially reflecting an energy conservation mechanism. Bornean orang-utans are extremely well-adapted to low fruit availability. This is reflected in their extremely low levels of energy expenditure (Pontzer et al., 2010) and their energy-efficient locomotion style (Roth et al., 2017; Thorpe et al., 2007). This inclination to conserve energy may also manifest in their behaviour during our experiment. In the preference tasks, the locations of the dots was randomized in a circular way between trials, with both dots appearing in exact opposite position equidistant from the center of the screen. While this approach helped to avoid anticipatory clicking by the orang-utans, it did result in differential energy costs associated with the dots. Clicking the dot in the upper portion of the screen required them to lift their arm further compared to clicking the dot in the lower portion of the screen. Consequently, the orang-utans were more inclined to select the dot in the lower portion of the screen. It is important to acknowledge this limitation in our experimental design. Nevertheless, even after accounting for the vertical location of the dots, we found no bias for flanged or unflanged stimuli (Supplementary Table 4). Thus, the strong urge of orang-utans to conserve as much energy as possible may influence their performance during cognitive tasks.

Future studies on orang-utan cognition should consider the aforementioned effects of colour and dot location on choices. These biases underscore the need for a biocentric approach to animal cognition, which takes into account a species' uniquely adapted perceptual system (Bräuer et al., 2020). Interestingly, however, the notion that orang-utans try to conserve energy during cognitive tasks opens up intriguing avenues for further research. If orang-utans are so prone to conserve energy, it might be possible to exploit this tendency by presenting them with an effort task. Previous studies with primates have developed effort paradigms that are relatively easy to use. These paradigms allow individuals to control the presentation of stimuli by holding a button (i.e., exerting effort). For example, previous studies have used this approach to study preferences for different stimulus categories in Japanese macaques (*Macaca fuscata*), finding that they exerted more effort to see stimuli of monkeys (Tsuchida & Izumi, 2009) or humans (Ogura & Matsuzawa, 2012). A similar design could be considered for orang-utans: given that energy conservation is such a core strategy for them, using an effort task may be an especially relevant method to induce their preferences for specific stimuli categories.

In conclusion, our findings from two experimental paradigms indicate no immediate attentional bias towards large flanges or symmetrical faces, nor a choice bias for flanged males. However, we did find a preference for the colour red in the preference task. Furthermore, individuals seemed to conserve energy during the preference task by picking the vertically lowest option on the touchscreen. Our results highlight the importance of taking species-specific characteristics into account when designing cognitive experiments. Future studies could leverage the energy-conserving nature of Bornean orang-utans by presenting them with effort tasks, where they need to exert effort to view stimuli. Such an approach may be fruitful to study social cognition, including its interplay with mate choice, in Bornean orang-utans.

Chapter 7

Orang-utans like it cheeky: Attentional bias towards flanged males in Bornean orang-utans (*Pongo pygmaeus*)

Abstract

The selection of a mate is a decisive choice that carries substantial weight in an individual's fitness. As a result, individuals may employ various cognitive mechanisms to navigate the mate selection process effectively. These mechanisms, such as preferential attention towards attractive conspecifics or traits, have been widely studied in humans. However, only a few studies have investigated these mechanisms in non-human primates. To address this gap, we conducted two eye-tracking experiments with four zoo-housed Bornean orang-utans (*Pongo pygmaeus*), a species that is characterised by extreme sexual dimorphism. In both experiments, using naturalistic and controlled stimuli, we found that orang-utans exhibit an attentional bias towards males with fully developed flanges, a sexually dimorphic trait carried by some adult males. Importantly, this attentional bias was apparent in both immediate and voluntary attention. By revealing the presence of attunement towards mating-related traits in the attentional mechanisms of a great ape species, our findings not only contribute to the growing body of knowledge on the cognitive basis of mate choice but also open up avenues for future research into the interplay between mate choice and cognition in non-human primates.

Based on:

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/BU1XYR

Introduction

Mate selection is a crucial process for sexually reproducing animals. The choice of a mate fundamentally defines an individual's biological fitness: picking a good partner can ensure that genes are well represented in the following generation, whereas picking a bad partner can cause genes to disappear from the population (Buss & Schmitt, 2019). Numerous species have evolved certain preferences that direct them when selecting a partner as a result of this significant motivation to do so (Rosenthal, 2017). Thus, these motivations influence cognition. In humans, for instance, various cognitive processes such as visual attention seem to be affected by sexual selection, and these processes can aid in identifying suitable mates or competitors (Maner & Ackerman, 2015). However, relatively little is known about the cognitive underpinnings of mate selection in other animals. In the current study, we investigated whether Bornean orang-utans, a species characterised by extreme sexual dimorphism (Utami Atmoko et al., 2008), showed an attentional bias towards fully developed flanged males.

The interplay between sexual selection and visual attention has been extensively studied in humans. Many studies have found that heterosexual women and men have an attentional bias towards attractive members of the opposite sex (Leder et al., 2016; Mitrovic et al., 2018; Roth et al., 2022, 2023). Similarly, humans also show vigilance toward attractive same-sex individuals (Maner et al., 2009). Importantly, such attentional biases have been identified for both immediate (e.g., Roth et al., 2022) and voluntary attention (e.g., Leder et al., 2016; Roth et al., 2023). Immediate attention constitutes automatic orienting towards relevant stimuli such as fear-inducing animals (Shibasaki & Kawai, 2009) or faces (Kawai et al., 2016). The typical measurement used to assess immediate attention is the time it takes for a participant to attend to any given stimulus after its onset. Voluntary attention reflects the deliberate and self-directed allocation of attentional resources to stimuli (Souto & Kerzel, 2021) and is typically measured as a function of the total time that participants spend looking at any given stimulus (Roth et al., 2023). In humans, attentional biases towards attractive faces also seem to extend to sexual dimorphism: both men and women seem to have a visual bias for more masculine male faces (Garza & Byrd-Craven, 2023; Yang et al., 2015). Interestingly, this is not only the case in humans: rhesus macaque (*Macaca mulatta*) females look significantly longer at the more masculine faces of conspecifics (Rosenfield et al., 2019). This implies that attentional biases towards such sexually selected traits can also be found in non-human primates.

In the last two decades, an increasing number of studies have investigated sustained attention and its relation to sexual selection in primates, mostly using a preferential looking paradigm (Winters et al., 2015). In this paradigm, individuals are confronted with different types of pictures presented simultaneously during each trial, and the relative attention to each stimulus is used as a proxy for interest. Many of the studies on this topic have been performed with rhesus macaques. Seminal work by Waitt et al. (2003, 2006) employing a preferential looking paradigm established that macaque females had an attentional bias towards bright red male faces when they were paired with paler faces, while males had an attentional bias towards bright red female hindquarters, but not faces. More recently, researchers have elaborated on these studies by testing free-roaming rhesus macaques. For instance, Dubuc et al. (2016) found that macaques had a bias for red male faces, whereas Rosenfield et al. (2019) identified an attentional bias for more masculine male faces. Thus, the preferential looking paradigm has been successfully used to study the interaction between sexual selection and attentional processes in primates.

The above-mentioned studies mostly relied on video recordings of participants combined with frame-by-frame analysis to determine gaze direction. Partly because this is an extremely time- and labour-intensive method, many recent studies on captive primates have used eye tracking. An eye tracker has infrared cameras specialized for the automatic and accurate detection of eye movements and gaze patterns to study primate social cognition (Hopper et al., 2021; Lewis & Krupenye, 2022). Recently, some studies have employed eye tracking to study the interaction between visual attention and sexual selection in primates. For example, Damon et al. (2019) used eye tracking to establish that rhesus macaques show an own-species bias for attractive faces similar to humans (Damon et al., 2019). Additionally, Lonsdorf et al. (2019) showed that brown-tufted capuchin monkeys (*Sapajus apella*), both male and female, were especially attentive towards pictures of same-sex individuals instead of opposite-sex individuals, suggesting that capuchin monkeys were more interested in potential competitors than potential mates. Thus, previous studies in primates have established that eye tracking can successfully elucidate attentional biases in the context of sexual selection.

To date, most studies have focused on macaques. However, to fully understand the evolutionary underpinnings of such attentional biases, it is important to test a wide range of species (Smith et al., 2018), ideally with different mating systems

(Petersen & Higham, 2020). Some primate species, such as orang-utans (*Pongo* spp.), exhibit extreme forms of sexual dimorphism that are thought to be the result of both intense male-male competition and female choice (Utami Atmoko et al., 2008). In addition, these arboreal great apes are characterised by male bimaturism, meaning that there are two distinct types of male morphs: unflanged males and flanged males (Utami et al., 2002). Unflanged males experience arrested development. They are sexually mature and produce offspring but are not preferred mates for adult females (Knott et al., 2009; Kunz et al., 2022). However, flanged males have fully developed secondary sexual characteristics such as an extremely large body size, long hair, a large throat sac, and conspicuous flanges on the sides of their faces (Kunz et al., 2022). Furthermore, ovulating females prefer mating with flanged males (Knott et al., 2009). Female choice for flanged males potentially reflects selection for good genes because the transition from unflanged to flanged males is energetically costly (Knott, 2009). Moreover, flanged males exhibit mutual aggression, and fights between flanged males can lead to serious bodily harm. Thus, by mating with flanged males, orang-utan females may select for males of good genetic quality.

In this study, we investigated whether Bornean orang-utans have an immediate and sustained attentional bias towards flanged males. In the first experiment, we presented unique paired portraits of one flanged male and one unflanged male. If flanges were indeed a source of information for orang-utans, we expected the participating orang-utans to (i) gaze immediately at the portrait of the flanged male and (ii) spend relatively more time looking at the flanged male within each trial. In our second experiment, we extended our first experiment by presenting naturalistic stimuli (i.e., different perspectives and natural poses, including other parts of the body in addition to the face) of four different male orang-utans (two flanged, two unflanged) in all possible combinations. This allowed us to investigate whether the results from Experiment 1, with more controlled stimuli, would hold for more naturalistic stimuli. Furthermore, it allowed us to explore how orang-utans divide their attention when presented with two stimuli of males of the same morph and whether they have looking biases for specific individuals over others.

Method

Subjects and housing

Our sample included four adult Bornean orang-utans (*Pongo pygmaeus*; females: Samboja, Sandy, Wattana; male: Amos) that lived in a fission-fusion enclosure with four other orang-utans (one of which was transferred during the study period; Table 1) in Apenheul Primate Park (Apeldoorn, The Netherlands). The females, but not the male, had prior experience with touchscreen-based research. However, none of the individuals had experience with eye tracking.

The orang-utans were housed in a building consisting of four indoor enclosures that were each connected to outdoor islands. The orang-utans were typically housed in 3-4 subgroups and group composition was sometimes changed with the aim of mimicking the natural social structure of orang-utans, in which they form temporary parties but no stable social groups. Some individuals never shared enclosures to avoid conflict (e.g., two adult males). The test setup was located in one of their night enclosures, out of view of the public. The setup was accessible from two of the indoor enclosures. Testing took place between March and August 2022 on Tuesdays and Fridays between 11.00 and 13.00.

Table 1. Overview of the Apenheul orang-utans.

Name	Sex	Date of birth	Origin	Participating?	Calibration accuracy (precision)
Kevin	M	~1982	Wild	No	
Sandy	F	29-4-1982	Captive	Yes	2.1mm (2.3mm)
Wattana	F	17-11-1995	Captive	Yes	0.5mm (2.3mm)
Amos	M	20-12-2000	Captive	Yes	0.4mm (5.0mm)
Samboja	F	9-6-2005	Captive	Yes	0.1mm (1.3mm)
Kawan (until 20-6-2022)	M	22-2-2010	Captive	No	
Baju	M	2-12-2015	Captive	No	
Indah	F	19-10-2017	Captive	No	

Experiment 1

Procedure

Participants were calibrated and tested using Tobii Pro Lab v. 1.194 and a Tobii Pro Spectrum with a sampling frequency of 1200Hz that was attached to a 24” monitor (16:9, 1920x1080). The monitor was placed behind a 1.2 cm thick polycarbonate panel with a drinking nozzle. Throughout calibration and testing, we used the great ape eye tracking mode on the eye tracker. On the top of the screen, we added a webcam to record the participants during the test sessions.

First, we calibrated the participants using a resizing video as a calibration target in Tobii Pro Lab. We used a range of different videos during the calibration process, depicting caretakers, baby orang-utans, food, and mating orang-utans. The calibration process was repeated until a successful calibration was obtained, and this calibration was reused during the experiment. With Sandy, we managed to obtain a successful 5-point calibration, whereas the other orang-utans completed a successful 2-point calibration, which is sufficient to produce accurate gaze data for this type of experimental design (Hopper et al., 2021).

After the calibration phase, data collection began. Each participant completed nine sessions of six trials (54 trials in total). Each session started with a 9-point grid to visually inspect calibration accuracy. Thereafter, six trials were started. Each trial started with a fixation video in the center of the screen (180 × 180 pixels) depicting one of the orang-utan caretakers. Stimulus presentation was started manually; when the eyetracker showed that the participant's gaze overlapped with the fixation video, the experimenter proceeded to the stimuli, which were presented for four seconds. After the stimulus presentation, a gray screen was shown for three seconds. After all six trials were completed, the experiment was automatically stopped. Participants completed a maximum of three sessions on testing days, and the order of the sessions was randomized between participants.

After the participants had completed all nine sessions, we repeated trials in which the participant (i) looked away from the center during trial onset because the start point of the trial would not be neutral, or (ii) showed less than 1s of fixation time on the stimuli during the trial because this could indicate a lack of attention and/or distraction during the trial. During the experiment, the orang-utans were rewarded with strongly diluted (±1:35) sugar-free raspberry lemonade.

Stimuli

In each trial, two stimuli, 690 × 500 pixels each, were presented: one flanged face and one unflanged face on a light-gray background (#808080). The stimuli were centered at 20% and 80% horizontally and 50% vertically on a dark-gray background (#626262). The stimuli were collected from the Internet, mainly from release reports published by Bornean orang-utan reintroduction programs. These were supplemented with portrait pictures taken from semi-wild orang-utans and pictures of zoo-housed orang-utans within the orang-utan EEP.

We checked for differences in luminance and contrast between stimuli using a custom MATLAB script to determine luminance and contrast for each stimulus, and then calculated the difference in luminance and contrast between the flanged and unflanged stimuli at the trial level. We found no robust differences in contrast (Bayesian intercept-only LM; 89% CrI [-0.08; 0.35], *pd* = 0.85) or luminance (Bayesian intercept-only LM; 89% CrI [-0.23; 0.21], *pd* = 0.53) between flanged and unflanged stimuli. This check ensured that gazing patterns were not driven mainly by low-level features at the stimulus level, which are known to capture visual attention (Theeuwes, 1995).

Experiment 2

Procedure

This procedure was identical to that used in Experiment 1. However, because of time pressure, we applied a maximum of four sessions per participant per test day instead of three. Experiment 2 consisted of 12 sessions of six trials in total, followed by repetition of erroneous trials, similar to Experiment 1.

Stimuli

Owing to an editing mistake, the dimensions of the stimuli for Experiment 2 were slightly different from those in Experiment 1. Each trial consisted of two stimuli of 600 × 450 pixels, centered at 22.5% and 77.5% horizontally and 50% vertically on a dark-grey background (#626262). While this meant that Experiments 1 and 2 were slightly different, the presentation of stimuli was administered in exactly the same way as in Experiment 2.

For Experiment 2, we selected six naturalistic stimuli of four different orang-utan males (two flanged: Bako & Sibu, two unflanged: Jingga & Wousan). Stimuli of Bako and Jingga were provided by Ouwehands Zoo (Rhenen, The Netherlands), stimuli of Sibu were provided by Dublin Zoo (Dublin, Ireland), and stimuli of Wousan (housed in Paignton Zoo, UK) were kindly shared by Brian Lilly. All four males were part of the orang-utan EEP and had not been previously housed with the subjects of the study. We selected four portrait photos and two photos depicting both the face and (part of the) body. Using GIMP (v2.10.32), we transformed each photo to grayscale and then applied the Equalize-option to standardise the luminance of all stimuli. We paired the stimuli such that participants were always presented with stimuli from the same category within a trial. Furthermore, we presented all possible combinations of males to the participants (four males, so six combinations) within one session.

Inter-rater reliability

All sessions of both experiments were scored by TR to check whether subjects looked away from the center of the screen during trial onset so that these trials could be repeated at the end. To test whether such trials could be reliably identified, TR and EvB coded eight sessions (48 trials) from Experiment 1 for looking away during trial onset. Of these 48 trials, they agreed to include 34 and excluded 10, but disagreed on inclusion of four trials, resulting in a Cohen's kappa of 0.78 (91.7% agreement), reflecting a good level of reliability between raters.

Statistical analysis

All analyses were performed using R Statistics Version 4.2.2 (R Core Team, 2023). For our analyses, we employed a Bayesian approach, which has become increasingly popular in recent years owing to its numerous advantages over frequentist analyses (Kruschke et al., 2012; Makowski et al., 2019). Whereas frequentist approaches, such as p-value null hypothesis testing, provide insight into the plausibility of the data under a particular hypothesis, Bayesian methods inform us about the credibility of our parameter values based on the observed data (Kruschke et al., 2012; McElreath, 2018). This difference is reflected in the contrasting interpretations of frequentist and Bayesian confidence intervals. While the former provides a range of values that contain the estimate over the long term, the latter identifies the most plausible parameter values given the data. Moreover, Bayesian methods allow the integration of prior expectations into the model, are less susceptible to Type I errors, and are more robust in small and noisy samples (Makowski et al., 2019). Taken together, these factors render Bayesian methods a valuable tool for data analysis.

All models were created in the Stan computational framework and accessed using the *brms*-package (Bürkner, 2017, 2018). All models were run with four chains and 6000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van de Schoot, 2017). No divergence or excessive autocorrelation was found.

First fixation

To investigate whether orang-utans had a first fixation bias toward flanged males when paired with unflanged males, we used binary logistic regression with the location of the first fixation (1=flanged male, 0=unflanged male) as the dependent variable. We modelled the dependent variable as a function of the *Intercept* and the *Location of the flanged male stimulus* (left/right on the screen) to control for potential side biases. To investigate the effect of different combinations of male morphs on first fixation, we created a binary variable reflecting the location of the first fixation (1=left, 0=right). We modelled this dependent variable as a function of the interaction between *the left stimulus morph* (flanged/unflanged) and *the right stimulus morph* (flanged/unflanged). In all analyses, we allowed Intercepts to vary by Subject, and Session nested in Subject.

For binary logistic regressions, we specified regularizing Gaussian priors with M = 0 and SD = 1 for the Intercept and independent variables. We used the default Student's *t* priors with 3 degrees of freedom for variance parameters.

After running the models, we used the *emmeans*-package (Lenth, 2023) to provide estimates based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects. First, we report the median estimate *b* and the median absolute deviation of the estimate between square brackets. Second, we report an 89% credible interval for the estimate (89% CrI). We chose 89% instead of the conventional 95% to reduce the likelihood that the credible intervals would be interpreted as strict hypothesis tests. Instead, the main goal of credible intervals is to communicate the shape of posterior distributions (McElreath, 2018). Third, we report the probability of direction (*pd*), that is, the probability of a parameter being strictly positive or negative, which varies between 50% and 100% (Makowski et al., 2019).

Total fixation duration

To investigate total fixation duration, we used a zero-one inflated beta model, which is suitable for continuous proportions containing zeros and ones (Ospina & Ferrari, 2012). These models consist of multiple components: a beta component to describe the values between 0 and 1, and two binary components to predict the occurrence of zeros and ones. Zero-one-inflated beta regression has previously been employed in eye-tracking studies (e.g., Chiquet et al., 2021). For each trial, we calculated a *Looking time bias*-score. In Experiment 1 and the replication of this experiment in Experiment 2, we calculated this bias by dividing the fixation time on the flanged male stimulus by the sum of the fixation times on the flanged and unflanged stimuli.

Thus, the *Looking time bias*-score represents the proportion of the total fixation time on the stimuli directed towards the flanged male stimulus. In Experiment 2, we also explored how the orang-utans divided their attention when presented with two stimuli of males of the same morph compared to when presented with males of different morphs. Because we could not calculate a *Looking time bias*-score in the same way as described above, because in some trials there were either two flanged male- or no flanged male-stimuli, we calculated the score differently for this analysis. We used the location of the photos as a reference point to calculate the looking time bias by calculating the bias toward the left picture (Roth et al., 2023). Hereafter, we tested whether this bias is affected by the stimulus category on the left side and right side on the screen.

To study whether orang-utans had an attentional bias toward flanged males, we modelled *Looking time bias*-score as a function of the *Intercept* and the *Location of flanged male stimulus* (left/right on the screen) to control for potential side biases. To investigate the effect of different combinations of male morphs on orang-utan attention, we modelled the *Looking time bias*-score as a function of the interaction between *Left stimulus morph* (flanged/unflanged) and *Right stimulus morph* (flanged/unflanged). The same model formulas were specified for all four model components (*mu, phi, zoi, and coi*). In all analyses, we allowed Intercepts to vary by Subject, and Session nested in Subject. Furthermore, we weighed each trial by the total fixation duration on the stimuli combined in that trial relative to the subject's average. Thus, trials in which the orang-utans paid more attention to the screen had a larger weight in the analysis. In this manner, we avoided that trials where the orang-utans were relatively distracted or disinterested would have a large influence on the outcome of our analysis.

To explore whether we could find attentional biases towards specific males in Experiment 2, we calculated a *Looking time bias*-score for each stimulus in each trial, reflecting the proportion of total fixation duration that the orang-utan fixated on stimuli depicting a specific individual. We constructed three separate models: one for each female. Due to computational issues, we could not construe an individual preference-model for the male participant, Amos. Within each model, we modelled *Looking time bias* as a function of *Individual of interest* (Bako, Sibu, Jingga or Wousan) and *Other individual presented* (Bako, Sibu, Jingga or Wousan), to control for the effect of the second stimulus. We allowed the Intercept to vary by session.

For the zero-one inflated beta models, we used a Gaussian prior with $M=0$ and $SD=1$ for the Intercept of the beta component of the model and for all independent variables. This also applied to the independent variables in the formulas for *phi, coi*, and *zoi*. For all variance parameters, we kept the default Student's *t* priors with 3 degrees of freedom. Furthermore, we kept the default logistic priors for the Intercepts of *zoi* and *coi*, and default Student's *t* prior with 3 degrees of freedom for the Intercept of *phi*.

After running the models, we used the *emmeans*-package (Lenth, 2023) to integrate the different model components and to provide estimates based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects (see "First fixation").

Ethics statement

This study employed only non-invasive methods, and animals were not harmed or punished in any way during the study. Participation was voluntary, animals were tested in a social setting, and animals were never deprived of food or water. The care and housing of the orang-utans adhered to the guidelines of the EAZA Ex-situ Program (EEP). Furthermore, our research complied with the ASAB guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2023), was carried out in accordance with the national regulations, and was approved by the zoological management of Apenheul Primate Park (Apeldoorn, The Netherlands).

Results

Experiment 1

First fixation

The outcomes of the Bayesian binary logistic regression (Supplementary Table 1; see Appendix G for model stability checks) suggested that the orang-utans had a first fixation bias towards flanged male stimuli ($b_{Intercept}$ = 0.599 [0.033], 89% CrI [0.546; 0.651], *pd* = 0.998). However, this was not the case for all individuals (Figure 1A): Amos ($b_{Intercept}$ = 0.690 [0.066], 89% CrI [0.586; 0.787], *pd* = 0.999) and Sandy ($b_{Intercept}$ = 0.641 [0.059], 89% CrI [0.548; 0.733], *pd* = 0.994) showed a robust bias towards flanged male stimuli, while this was not the case for Samboja ($b_{Intercept}$ = 0.512 [0.073], 89% CrI [0.403; 0.627], *pd* = 0.565) and Wattana ($b_{Intercept}$ = 0.557 [0.064], 89% CrI [0.450; 0.650], *pd* = 0.800). Furthermore, we found that the orang-utans had a leftward bias: they were more likely to first fixate on the flanged male stimulus if it was on the left side of the screen ($b_{left\text{-}right}$ = 0.332 [0.064], 89% CrI [0.226; 0.433], *pd* = 1.00).

Total fixation duration

The outcomes of the Bayesian zero-one inflated beta regression (Supplementary Table 2; see Appendix G for model stability checks) suggested that the orang-utans had an attentional bias towards flanged male stimuli ($b_{Intercept}$ = 0.575 [0.024], 89% CrI [0.538; 0.615], *pd* = 0.999). Again, this was not the case for all individuals (Figure 1B): for Amos ($b_{Intercept}$ = 0.596 [0.038], 89% CrI [0.536; 0.656], *pd* = 0.996) and Wattana ($b_{Intercept}$ = 0.608 [0.040], 89% CrI [0.544; 0.671], *pd* = 0.997) we found a clear bias. For Sandy it was less pronounced ($b_{Intercept}$ = 0.574 [0.046], 89% CrI [0.498; 0.645], *pd* = 0.942), whereas Samboja showed no clear bias ($b_{Intercept}$ = 0.525 [0.046], 89% CrI [0.449; 0.596], *pd* = 0.700). Furthermore, we found no side bias, meaning that the location of the flanged male stimuli (left or right on the screen) did not modulate the bias towards flanged males ($b_{left\text{-}right}$ = 0.033 [0.045], 89% CrI [-0.036; 0.104], *pd* = 0.773).

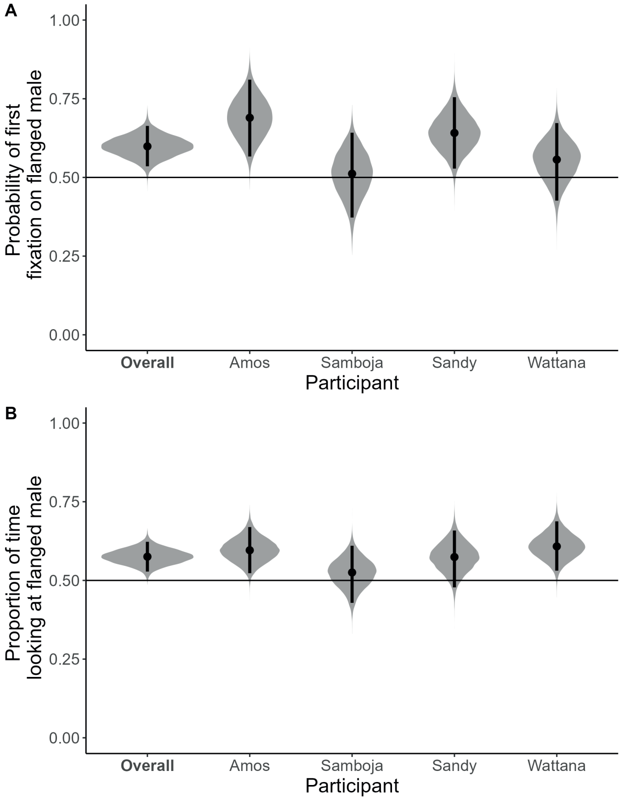


Figure 1. Results of Experiment 1 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

Experiment 2

Replication first fixation

Similar to Experiment 1, the outcomes of the Bayesian binary logistic regression (Supplementary Table 1) suggested that the orang-utans had a first fixation bias towards flanged male stimuli ($b_{Intercept}$ = 0.582 [0.039], 89% CrI [0.520; 0.645], *pd* = 0.981). Although all individuals showed a bias in the expected direction, the finding was not robust for all four orang-utans (Figure 2A) Amos ($b_{Intercept}$ = 0.596 [0.057], 89% CrI [0.504; 0.694], *pd* = 0.955) and Sandy ($b_{Intercept}$ = 0.601 [0.057], 89% CrI [0.509; 0.698], *pd* = 0.963) showed a more robust first fixation bias than Samboja ($b_{Intercept}$ = 0.585 [0.056], 89% CrI [0.489; 0.678], *pd* = 0.925) and especially Wattana ($b_{Intercept}$ = 0.549 [0.064], 89% CrI [0.436; 0.648], *pd* = 0.756). In addition, we again found that the orang-utans had a leftward bias ($b_{left\text{-}right}$ = 0.195 [0.072], 89% CrI [-0.079; 0.309], *pd* = 0.997), although it was less pronounced than in Experiment 1.

Replication total fixation duration

Similar to Experiment 1, the outcomes of the Bayesian zero-one inflated beta regression (Supplementary Table 2) suggested that the orang-utans had an attentional bias towards flanged male stimuli ($b_{Intercept}$ = 0.607 [0.028], 89% CrI [0.564; 0.653], *pd* = 1.000). However, in contrast to Experiment 1, all four orang-utans had a robust bias towards flanged males (Figure 2B): Amos ($b_{Intercept}$ = 0.593 [0.032], 89% CrI [0.541; 0.645], *pd* = 0.997), Samboja ($b_{Intercept}$ = 0.597 [0.036], 89% CrI [0.540; 0.656], *pd* = 0.995), Sandy ($b_{Intercept}$ = 0.625 [0.054], 89% CrI [0.542; 0.715], *pd* = 0.991), and Wattana ($b_{Intercept}$ = 0.613 [0.048], 89% CrI [0.526; 0.690], *pd* = 0.978). Furthermore, similar to Experiment 1, we found no side bias ($b_{Intercept}$ = 0.002 [0.049], 89% CrI [-0.073; 0.085], *pd* = 0.519).

Full dataset

With regard to the first fixation duration, we found that probability of first fixation on the left stimulus depended on the combination of stimuli (Supplementary Table 3; Figure 3A; see Appendix G for model stability checks). First, in line with our previous analyses, the orang-utans had an overall left bias for first fixation (b = 0.604 [0.029], 89% CrI [0.558; 0.651], *pd* = 1.000). Second, we found a difference in probability of first fixation on the left stimulus between trials where a flanged male was presented on the left with an unflanged male on the right, and an unflanged male on the left with a flanged male on the right ($b_{FM.UFM\text{-}UFM.FM}$ = 0.164 [0.063], 89% CrI [0.064; 0.263], *pd* = 0.996). However, probability of fixating on the left stimulus first did not differ robustly between any of the other conditions (Supplementary Table 5).

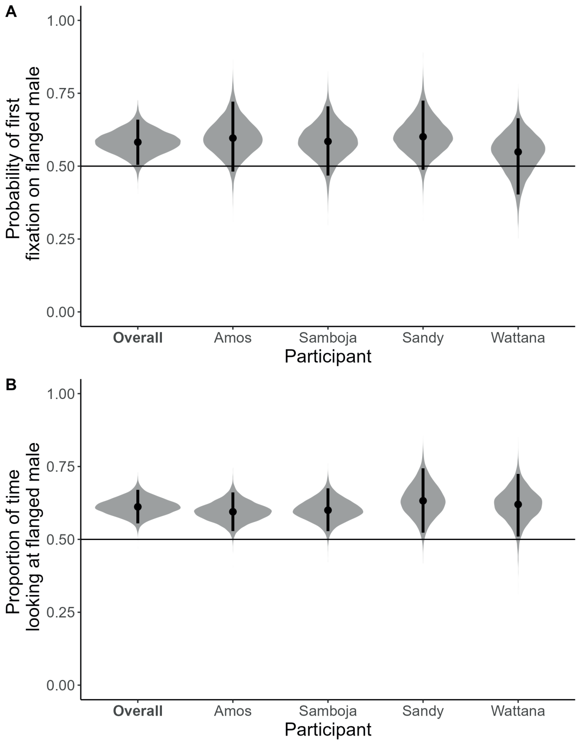


Figure 2. Results of the replication of Experiment 1 in Experiment 2 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

With regard to the total fixation duration, we found that the interaction between morph of the left stimulus and morph of the right stimulus predicted looking time bias towards the left stimulus (Supplementary Table 4; Figure 3B; see Appendix G for model stability checks). If a flanged male and unflanged male stimulus were paired, the bias deviated robustly from 0.5 (flanged left-unflanged right: *b* = 0.588 [0.030], 89% CrI [0.540; 0.636], *pd* = 1.000; unflanged left-flanged right: *b* = 0.427 [0.028], 89% CrI [0.382; 0.473], *pd* = 0.996). However, this was not the case when two males of the same morph were shown (flanged-flanged: *b* = 0.521 [0.041], 89% CrI [0.455; 0.585], *pd* = 0.702; unflanged-unflanged: *b* = 0.505 [0.039], 89% CrI [0.440; 0.567], *pd* = 0.556). The pairwise contrasts confirmed this pattern, although not all of them were robust (Supplementary Table 5).

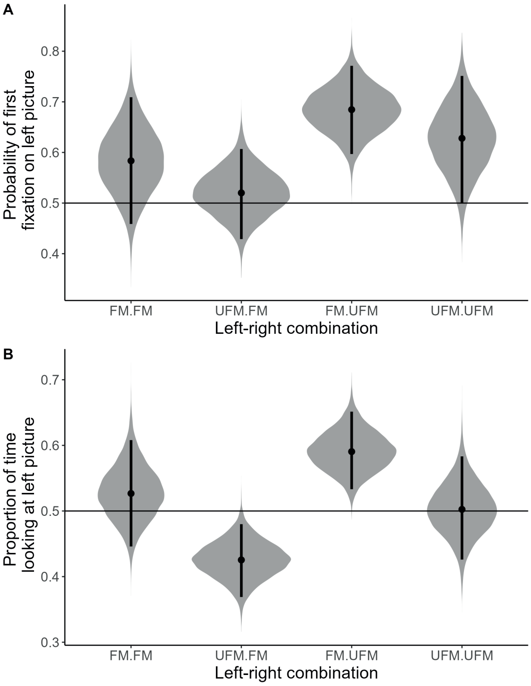


Figure 3. Results of Experiment 2 depicting (A) predicted probability of fixating first on the left stimulus and (B) predicted proportion of time spent fixating on the left stimulus as a function of the morph depicted on the left and right side of the screen. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

Individual preferences

For the three female participants, we constructed individual models to test whether they had robust attentional biases towards stimuli depicting specific males (Supplementary Table 6). For Samboja, we found that she spent the largest proportion of time fixating on pictures of Sibu, a flanged male, and the lowest proportion of time fixating on Jingga, an unflanged male (Figure 4). Pairwise contrasts revealed that the difference in attention towards Sibu and Jingga was robust ($b_{Jingga\text{-}Sibu}$ = -0.127 [0.064], 89% CrI [-0.228; -0.024], *pd* = 0.976). Other contrasts revealed no robust differences, although Samboja tended to prefer Bako over Jingga (Supplementary Table 7). For Sandy, we found that she spent the largest proportion of time fixating on Bako, a flanged male, while she spent the lowest amount of time fixating on Wousan, an unflanged male (Figure 4). Pairwise contrasts revealed that this difference was robust ($b_{Bako\text{-}Wousan}$ = 0.142 [0.078], 89%

CrI [0.015; 0.265], *pd* = 0.964). While other contrasts revealed no robust differences, Sandy tended to prefer Bako to Jingga (Supplementary Table 7). Lastly, Wattana had no clear preference: she spent most time fixating on Bako, closely followed by Jingga and Sibu. Interestingly, she spent the least amount of time fixating on Wousan compared with the other three males (Figure 4). However, pairwise contrasts revealed a clear difference only between Bako and Wousan ($b_{Bako\text{-}Wousan}$ = 0.156 [0.090], 89% CrI [0.011; 0.294], *pd* = 0.960). Furthermore, Wattana tended to prefer both Sibu and Jingga over Wousan (Supplementary Table 7).

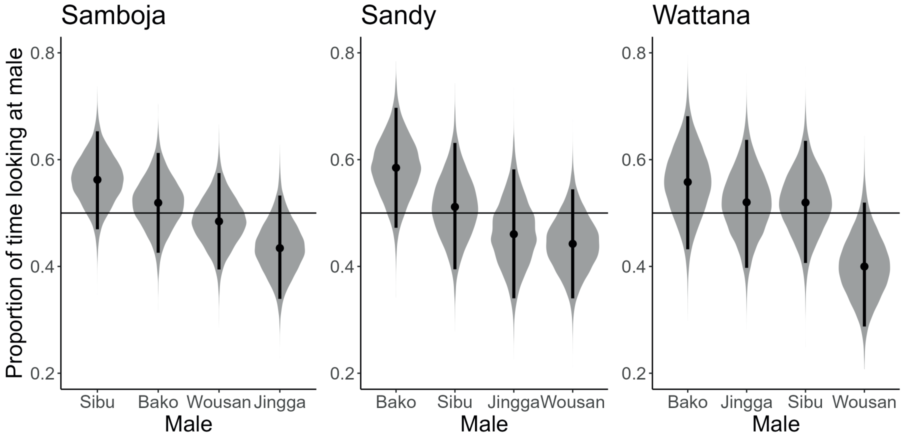


Figure 4. Results of the individual preference-models based on Experiment 2. The figures depict which male received most attention for each female participant separately. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

Discussion

The effect of facial characteristics on attentional processes in a mate choice context has been extensively studied in humans (Leder et al., 2016; Roth et al., 2022, 2023; Yang et al., 2015). However, relatively few studies have explored this topic in primates. In this study, we investigated how fully developed secondary sexual characteristics affect attentional processes in Bornean orang-utans. This arboreal great ape species is an ideal model for studying the effect of secondary sexual characteristics on attention processes because they are characterised by male bimaturism, meaning that adult males exist in two distinct morphs: unflanged males, who are reproductively active but not fully developed, and flanged males, which are morphologically distinct from adult females and unflanged males, and are preferred partners of females (Knott et al., 2009; Utami et al., 2002). Here, we presented four Bornean orang-utans with flanged and unflanged stimuli (Experiment 1) or combinations of different morphs, that is, flanged-flanged, unflanged-unflanged, or flanged-unflanged (Experiment 2), while we non-invasively tracked their gaze. Across two experiments, we found that the orang-utans were more likely to first fixate on stimuli depicting flanged males, and spent longer fixating on flanged male stimuli. Furthermore, we found that orang-utans had an immediate attentional bias toward the left side of the screen. Below, we discuss our findings in the context of human and primate literature on attention and provide suggestions for future research.

In two separate experiments, we discovered that orang-utans exhibited a higher likelihood of immediately fixating on stimuli depicting a male with flanges. This attentional bias towards flanges is in line with the general phenomenon of immediate attention towards evolutionarily relevant stimuli. By immediately detecting and processing biologically salient stimuli, an individual can effectively cope with situations that are relevant to their biological fitness (Carretié, 2014; New et al., 2007). Accordingly, humans have been found to immediately attend to the emotional expressions of conspecifics (Carretié, 2014; Kret & van Berlo, 2021; van Berlo et al., 2023), potential threats (Öhman et al., 2001), and attractive conspecifics (Lindell & Lindell, 2014; Roth et al., 2022, 2023). Similarly, recent evidence suggests that primates also immediately attend to biologically salient stimuli such as emotional scenes (King et al., 2012; Kret et al., 2016; van Berlo et al., 2023; but see Laméris et al., 2022). Our results suggest that immediate attentional bias may also be present for stimuli that are relevant to mate choice in primates.

Immediate attention is mostly driven by bottom-up processes and low-level stimulus properties (Theeuwes, 2010). We attempted to control for luminance and contrast at the stimulus level by comparing the luminance and contrast of flanged and unflanged stimuli in Experiment 1 and standardizing the stimuli in Experiment 2. However, local differences in contrast and luminance within stimuli may have affected immediate attention and influenced our results. Nonetheless, it is important to emphasise that differences in low-level properties, such as contrast, may provide a perceptual mechanism that makes specific traits stand out (Rosenfield et al., 2019). Therefore, rather than an alternative explanation, low-level properties may be the mechanism by which attention is attracted to biologically meaningful traits. In general, sexual selection favours traits that exploit the sensory system of receivers because a salient trait should stand out against environmental noise (Ryan & Cummings, 2013). Orang-utan flanges may be an example of a trait that exploits the sensory system of receivers for sexual selection purposes. Their unique flanged features may stand out, making them more salient to their potential mates. This may explain why orang-utans fixated first on stimuli depicting a male with flanges in our experiments, as these stimuli stood out against background noise due to their distinct low-level properties.

We also found that the orang-utans exhibited a first fixation bias towards the left stimulus in both experiments irrespective of the type of stimulus that was shown on the left. These results are consistent with those of previous human experiments. For instance, a study on attractiveness bias in humans found that 82% of the first fixations were directed towards the left face when two faces were paired (Leder et al., 2016). Importantly, this bias does not appear to be restricted to humans. Guo et al. (2009) presented facial stimuli to humans, dogs (*Canis lupus familiaris*), and rhesus macaques, and found that these species have a strong left bias in their first fixation when presented with faces. However, this bias may extend beyond the faces. In humans, it seems that an initial attentional bias towards the left visual field can be found across contexts, which suggests a more general perceptual bias driven by asymmetries in the attentional system between the two brain hemispheres (Ossandón et al., 2014). Overall, our findings regarding the first fixation of orang-utans suggest that they also have a perceptual bias towards the left during their first fixation. It is essential to consider this when designing studies to explore immediate attention in primates.

With regard to voluntary attention, we found that orang-utans fixated on flanged male faces for a larger proportion of each trial than on unflanged male faces across the two experiments. While immediate attention is mainly driven by automatic bottom-up attentional processes, the results for the total fixation duration were probably more reflective of top-down attention because the orang-utans could actively and voluntarily divide their attention during the four seconds that each trial lasted (Theeuwes, 2010). Therefore, it seems that the orang-utans volitionally fixated more on the flanged male faces than on the unflanged males. These results complement those of a previous study where it was shown that when scanning faces, orang-utans pay attention to the flanges (Kano et al., 2012). Furthermore, these results are in line with those of previous studies in humans and macaques. Previous research has shown an attentional bias for masculinity in male faces in humans (Garza & Byrd-Craven, 2023; Yang et al., 2015). Additionally, a study in rhesus macaques showed that females prefer to look longer at a more masculine male face in a pair of two (Rosenfield et al., 2019). In humans (Penton-Voak & Chen, 2004; Pound et al., 2009), and potentially also in rhesus macaques (Rhodes et al., 1997), facial masculinity is linked to testosterone levels. This is also seems to be the case for orang-utan flanges: males with higher testosterone levels developed flanges earlier than individuals with lower testosterone levels (Emery Thompson et al., 2012). Altogether, our study is the first to describe a voluntary attentional bias towards a masculine trait in a great ape species, suggesting that a preference for masculine traits that are under the control of testosterone is shared across different primate species. Furthermore, we show that this preference appears to be expressed at both early stages of visual processing as well as at later stages that involve volitional control.

One important caveat of our study is that we could not determine why orang-utans were more attentive to flanged males. They may have had more interest in flanged males because they are potential mating partners. Alternatively, their vigilance towards flanged males could be due to the potential threat they pose to infants due to infanticide risk (Beaudrot et al., 2009; Knott et al., 2019). Importantly, we also found a bias towards flanged males in the one male that participated in our study, suggesting that male competition could also cause an attentional bias towards flanged males. Future studies could focus more on this specific aspect using methods such as priming or testing at different points during the menstrual cycle of a fully cycling female orang-utan. If an attentional bias towards flanged males is driven by a willingness to mate with them by female orang-utans, we would expect to see a stronger bias during ovulation. This would be in line with previous research suggesting that females actively approach flanged males to mate with them during ovulation (Knott et al., 2009), thus showing concordance between cognition and behaviour.

However, very few studies have investigated ovulatory shift effects in non-human primates from a cognitive perspective, as such studies are difficult to conduct. In general, female primates in zoos and sanctuaries do not always have an active menstrual cycle as they are on birth control or have a dependent infant. To our knowledge, only one study has investigated the ovulatory shift effects in cognition in a non-human primate; Lacreuse et al. (2007)found evidence for increased attention towards, but not enhanced recognition of, male faces over female faces during the periovulatory period of rhesus macaques. Furthermore, recent studies in humans have also cast doubt on previously reported ovulatory shift effects in women because they have failed to find changes in mate attraction across the menstrual cycle (Stern et al., 2021) or a conclusive relationship between reproductive hormone levels and attention towards mate-relevant information such as facial masculinity (Garza & Byrd-Craven, 2023). Nonetheless, investigating the concordance between sexual motivation and attentional biases in orang-utans might help further elucidate the link between mate choice-relevant stimuli and visual cognition in non-human primates.

In Experiment 2, we presented the orang-utans with multiple unique stimuli of four Bornean orang-utan males. Given that the topic of variation in individual preferences of females has received relatively little attention in the past (Jennions & Petrie, 1997), we explored the individual attentional preferences of the three orang-utan females that participated in our study. While we found some robust differences in attention towards the four males at the individual level, all of these differences concerned pairs of flanged and unflanged males. Thus, we did not observe subtle attentional preferences, such as a preference for one flanged male over another. In general, studies on primate attention have mostly focused on differential attention towards specific stimulus categories, such as emotional versus neutral stimuli (Pritsch et al., 2017), familiar versus unfamiliar conspecifics (Hanazuka et al., 2013; Lewis et al., 2021), same-sex versus other-sex stimuli (Lonsdorf et al., 2019), or presence versus absence of facial characteristics (this study). However, we believe that it would be interesting for future studies to move beyond such classifications and look more into individual preferences. Admittedly, this would be a challenging endeavour that might require larger samples and more diverse stimulus sets. Nevertheless, it is relevant to explore such preferences, as studies in humans have already shown that humans exhibit considerable inter-individual differences in gaze patterns (Rogers et al., 2018) and that individual preferences for salient traits such as attractiveness are predictive of attention (Leder et al., 2016; Roth et al., 2023). One potential approach would be to employ reverse correlation techniques to create classification images per participant, which represent the face that attracts their attention. This technique has been widely applied to study human face perception (Dotsch & Todorov, 2012; Karremans et al., 2011) but has not yet been employed to study great ape cognition. Overall, while we found some individual differences in female attention towards male orang-utans, future research could benefit from a more individualized approach to examining primate attentional preferences.

To conclude, our study contributes to the understanding of how sexual selection shapes attentional processes by showing that Bornean orang-utans allocate their attention to a conspicuous sexually dimorphic trait, namely male flanges. We found this bias for both immediate and voluntary attention, which suggests that both bottom-up and top-down attentional processes are attuned to this facial characteristic. Thus, it seems that the visual system of great apes may be attuned towards stimuli that are relevant in the context of mate choice, as has been previously shown for humans. It is important that we cannot conclude why the orang-utans preferentially attended to flanged males: they might either be attracted to them or be vigilant. Therefore, we suggest that future work could make use of the natural fluctuations in mating motivation during the menstrual cycle. This would allow us to investigate whether the attentional bias towards flanged males increases as a function of mating motivation, which would suggest that the bias is driven by attraction. Overall, this study highlights the importance of understanding the role of sexual selection in shaping attentional processes, not just in humans but also in other great apes such as orang-utans, which may have implications for our understanding of the interplay between cognition and sexual selection.

Chapter 8

Evidence of female proceptive behaviour and vocalisation during ovulation in two zoo-housed Bornean orang-utan (*Pongo pygmaeus*) females

Abstract

In some primate species, females show changes in proceptive behaviour across the menstrual cycle. This anecdotal report discusses the occurrence of ovulation-induced proceptivity and vocalisations in two zoo-housed Bornean orang-utan females. Observations of two individuals, Temmy and Eloise, during their peri-ovulatory periods revealed distinct behavioral patterns. While Temmy demonstrated male-seeking behaviour and vocalisation in response to playbacks of male long calls, Eloise consistently solicited the male she was housed with and proactively produced vocalisations during her ovulation. Interestingly, the vocalisations produced by Temmy and Eloise seem to differ in many aspects from known orang-utan calls, although they bear some similarities to male long calls. Thus, the vocal repertoire of female orang-utans may be more extensive than previously thought. We carefully suggest potential functions of female proceptivity calls, while also outlining how such calls could be detrimental for orang-utan females. Furthermore, we consider the possibility that these vocalisations are only present in captive orang-utan populations.

Based on:

Roth, T. S., von Wulffen, C., Fox, M., Askew, J., Spierings, M., Perea-García, J. O. Evidence of female proceptive behaviour and vocalisation during ovulation in two zoo-housed Bornean orang-utan (*Pongo pygmaeus*) females. *Manuscript submitted for publication*.

Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/JNUTYU

Introduction

Primate females can substantially change their sexual behaviour across the menstrual cycle. According to Beach (1976), these changes in behaviour can be divided into three categories: attractivity, receptivity and proceptivity. Attractivity refers to the stimulus effect of the female on males. For example, genital swelling might increase attractivity of a female (Dixson, 2012). Proceptivity refers to female appetitive sexual behaviours, such as approaching males, vocalising, presenting, and affiliation with males. Receptivity concerns behaviours that facilitate copulation, such as employing the correct body postures (Hrdy & Whitten, 1986). In some primates, increases in attractivity, proceptivity and receptivity concord with the occurrence of ovulation. However, sexual behaviour in primates is not rigidly controlled by ovarian hormones and most female primates engage in mating throughout the menstrual cycle. Therefore, the relationship between fertility and sexual behaviour is not always straightforward in primates (Dixson, 2012).

Orang-utans (genus *Pongo*) are among the primate species for which there is evidence consistent with the idea that female sexual behaviour changes across their 30-day menstrual cycle. While recent evidence suggests that attractivity and receptivity do not change substantially across the cycle (Durgavich et al., 2023), data from both captive and field studies suggest that orang-utan females show a change in proceptivity across their menstrual cycle. In captivity, a zoo-housed Sumatran orang-utan (*Pongo abelii*) female showed a 4-6 day-lasting increase in proceptive behaviour, such as following, grooming, and touching the genitals of the male (Maple et al., 1979). According to the authors, these periods occurred approximately 26-30 days apart, which suggests that they coincided with ovulation. Similarly, in a restricted access study, orang-utan females were proceptive towards males specifically during their ovulation: when females had control over access to males, they chose to spend time with the male mostly during their ovulation (Nadler, 1995). Furthermore, field data suggest that Bornean orang-utan females (*Pongo pygmaeus*) show a qualitative change in proceptivity across their menstrual cycle (Knott et al., 2009): females seemed to make no distinction when mating with either flanged or unflanged males when they were not fertile, but specifically mated with dominant flanged males during ovulation. Altogether, these results suggest that orang-utans show qualitative and quantitative changes in proceptivity that co-occur with ovulation.

Orang-utans are also characterised by long calls: acoustic signals that are produced by flanged males or males who are developing flanges (Delgado et al., 2008). These calls reach a loudness of approximately 100 decibels (Lameira & Wich, 2008) and carry for about 1km (Mitani, 1985). These calls are thought to play an important role in regulating social interactions (Delgado et al., 2008), given that orang-utans are semi-solitary and only sporadically interact with conspecifics (Roth et al., 2020; van Schaik, 1999). Two main functions have been suggested, which are not mutually exclusive (van Schaik & van Hooff, 1996); first, long calls might facilitate inter-individual spacing, especially between males (Delgado et al., 2008; Mitani, 1985). Second, long calls might function to attract females (Mitra Setia & van Schaik, 2007). Accordingly, Mitra Setia & van Schaik (2007) reported that females approached male long calls, and especially the calls of local dominant males. Altogether, it seems that long calls do not only play a role in intrasexual competition, but also in intersexual competition.

When it comes to female vocalisations in the context of mating, remarkably few examples of proceptive vocalisations have been described in primates (Dixson, 2012). This also applies to orang-utans. Hardus et al. (2008) describe two vocalisations that females produce during copulation: mating squeals and fear squeals. However, we have found no mentions of proceptive vocalisations, i.e., vocalisations that precede mating events. Nonetheless, production of proceptive vocalisations might be beneficial for orang-utan females, through either coordinating movement with preferred males (long- or intermediate-distance calls) or communicating their intention or motivation to mate (short-distance calls) in order to reduce male ambivalence towards them (O'Connell et al., 2020). Especially in habitats with bad visibility vocalisations can aid in coordination and social interaction (Delgado, 2006) and reduce ambiguity during social approaches.

Here, we report two cases of increased proceptivity in ovulating zoo-housed Bornean orang-utan females. Our first case concerns Temmy, who showed a strong bodily and vocal response to male long call playbacks. We observed this phenomenon during a playback experiment in which she at first did not participate. She was temporarily housed in the outside enclosure while we conducted our playback experiment in the indoor enclosure, and was likely in her peri-ovulatory period. We opportunistically played long call recordings on 4 consecutive days while she was in the outdoor enclosure and videorecorded her behaviour. Approximately 2 months later, we repeated this on two consecutive days when she was most likely not ovulating. Our second case concerns Eloise, who appeared to produce long calls spontaneously during ovulation when she was still reproductively active. In this anecdotal report, we (1) describe the behaviours of Temmy and Eloise, and (2) describe the structure of their vocalisations.

Method

Temmy

Group and housing

Data for the first case were gathered in Allwetter Zoo (Münster, Germany). During the first study period (23-05-2022 until 27-05-2022), the zoo housed five adult Bornean orang-utans (4F, 1M; Supplementary Table 1). During the second study period (29-07-2022 until 30-07-2022) a new male was also present, who had recently been transported to the zoo. The orang-utan enclosure consisted of an indoor and outdoor enclosure, each capable of housing a subgroup. Alternatively, they could be connected to form one large enclosure.

Temmy, the female of interest in this case, had been living in Allwetter Zoo for over 20 years at the time of research. She had not been exposed to a flanged male since the death of the previous flanged male at the start of 2020. During the first study period, Temmy was housed solitarily in the outside enclosure until ±15.30, when Mr. Miyagi was also allowed to move to the outside enclosure. During the second study period, Temmy and unflanged male Mr. Miyagi were housed together (either in the indoor or the outdoor enclosure), while the rest of the group was already introduced to the new flanged male Ramon.

Female ovulation

While we lack hormonal evidence of ovulation, multiple lines of evidence suggest that Temmy was ovulating during our first observation period. Firstly, because of a breeding recommendation by the EEP, Temmy was not on contraceptives. Secondly, according to the curator and the orang-utan caretakers, Temmy started the peri-ovulatory period of her menstrual cycle right before the first study period. Thirdly, the caretakers had observed a cooperative mating event between Mr. Miyagi and Temmy on the evening of 22-05-2022, two days prior to the start of our study. While sexual activity is not restricted to the peri-ovulatory period, it is much more likely to occur during this period (Durgavich et al., 2023). In orang-utans, this part of the cycle lasts approximately 5 days, similar to humans (Kubatova & Fedorova, 2016).

Stimuli

The long call recordings that we used for the playback experiment were collected at Sikundur Research Station (Sumatra, Indonesia) by James Askew (Askew, 2019). From all the recordings, we selected only calls classified as "spontaneous". As control sounds we used two calls of the Great argus pheasant (*Argusianus argus*), a bird species that occurs in the natural habitat of orang-utans. We edited all stimuli to last 45 seconds so that each stimulus had the same duration. Furthermore, all recordings were normalized so that the volume level was similar across stimuli.

Design of trial

We made audio recordings of the vocal response using a Sennheiser ME 67 microphone and a Tascam DR-40X recorder. Two camcorders (study period 1) or one camcorder and one action camera (study period 2) were used to videorecord the behavioural response to the stimuli. To play the stimuli, we used a custom loudspeaker linked to a Marantz PMD 620 unit. We played the stimuli at ±90 dB at 1 m from the loudspeaker.

The setup of our study was in line with recommendations (Fischer et al., 2013): while one researcher was responsible for placing the speaker and playing the sound, one or two other researchers videorecorded the response. In addition, one of the researchers carried the microphone that was used to record Temmy's vocalisations opportunistically. Before starting a trial, we would first identify Temmy's location. After that, we would determine a suitable location for the speaker. We did not want the speaker to be clearly visible to Temmy at the onset of the trial. After we chose a location for the speaker, we would start the stimulus playback of 45s and immediately videorecord her response. We would continue videorecording her response for a few minutes after the stimulus ended, and would stop when her behaviour seemed to be back to baseline (ie., when she displayed no more intensely proceptive behaviours and/or stopped vocalising).

Eloise

Data for the second case were obtained from Los Angeles Zoo (LA, California, United States). This case concerns Eloise, a Bornean orang-utan female who was born in LA Zoo on 10th of November 1968, and has been living in LA Zoo since then. Over time, she has been housed with multiple individuals, including different males. She gave birth to 4 offspring from 3 different males between 1978 and 1987. In our case description, we focus on the period from 1999 until approximately 2018, date after which she is considered to be of post-reproductive age (based on the absence of a regular menstrual cycle). During the period that we describe, she was housed with a flanged male, and with different females. Furthermore, she was not on contraceptives at any time during this period.

Eloise has a condition similar to cerebral palsy, which she has had since birth. Her condition mostly affects her locomotion, since she has limited use of her hands and especially her feet. She has learned over her years how to modify her movements, and has generally locomoted by rolling or crawling. However, she has still been able to have a normal social life with conspecifics, and has been able to climb and manoeuvre throughout her exhibit space.

Importantly, one of the authors of this manuscript (MF) was Eloise’s primary caregiver in the zoo during the period that we describe.

Vocalisation analyses

Bioacoustic analyses were performed using Audacity software (Audacity Team, 2011). Measurements were taken of the total call length, inter-onset-intervals of the separate vocalisations, peak frequencies, and fundamental frequencies. Based on these parameters, the vocalisations of Temmy and Eloise were compared to other orang-utan calls obtained from *Orangutan network* of Universität Zurich (https://www.aim.uzh.ch/de/orangutannetwork.html; Hardus et al., 2009). Furthermore, we compared Temmy’s and Eloise’s call with male long calls recorded by James Askew (Askew, 2019; also see “Stimuli”).

Results

Temmy

Study period 1

On the first day (24-5-2022) that we performed a playback experiment in the indoor enclosure with all orang-utans except Temmy, we noted that Temmy showed a strong behavioural reaction through a semi-transparent door that connected the indoor and outdoor enclosure. On this first day, we played 3 control calls, 3 calls of flanged males, and 3 calls of transitioning males. Temmy showed up at the door during/after all playbacks of flanged male long calls, and once after playback of a transitioning male long call (Figure 1). Importantly, she would only come to the door during or after the playback of the long call. Thus, she was never visible at the window at the start of the trial. In addition, she never came to the door in response to the control sounds. Because of her strong reaction to the long call stimuli, we asked permission to opportunistically expose her to some stimuli in the outside enclosure. We started doing this on the afternoon of the first day.

Figure 1. Temmy coming to the door that separates the indoor and outdoor enclosure in response to a flanged male long call.

On the afternoon after we had finished with the indoor trials for the playback study, we played two long calls specifically to Temmy, in the outer enclosure. In both cases she showed a strong behavioural response (Figure 2). Her response to the long calls was characterised by fast movement in the direction of the speaker, climbing into climbing structures, and standing/sitting while looking in the direction of the speaker. Furthermore, Temmy started vocalising for multiple minutes in a row. On the morning of day 2, we resumed playing long calls to Temmy in the outside enclosure. However, we now also included control sounds to determine whether she would show the same behavioural response to all sounds. In total we played three long calls and four control sounds. Temmy showed responses similar to the day before when we played long calls, including vocalisations, but showed no discernible behavioural response when we played a control sound. Crucially, she quickly approached the source of the stimuli and emitted vocalisations in response to calls, but never to control sounds.

On the afternoon of day 2, we wanted to continue the experiment by playing more stimuli to Temmy. In this case, we played two long calls and two control stimuli. Similar to before, she did not respond to the control trials. However, her behavioural response to the long calls was completely different from this moment onwards. While she did still look into the direction of the speaker during the stimulus playback, she did not approach it like before, nor vocalise. In the next two days, we played three more long calls and three more control stimuli, but Temmy did not respond like she did on day 1 and the morning of day 2 anymore.

The change in behavioural response that we observed suggests that Temmy only showed proceptive behaviour in response to the calls during her peri-ovulatory phase. Given that this phase lasts about 5 days, this fits well with the fact that Temmy and Mr. Miyagi mated two days prior to the study period. However, another explanation would be that Temmy habituated to the stimuli over time, even though this would not explain why she did not show a similar response to the control stimuli. Still, we went back 2 months later to test this alternative hypothesis.

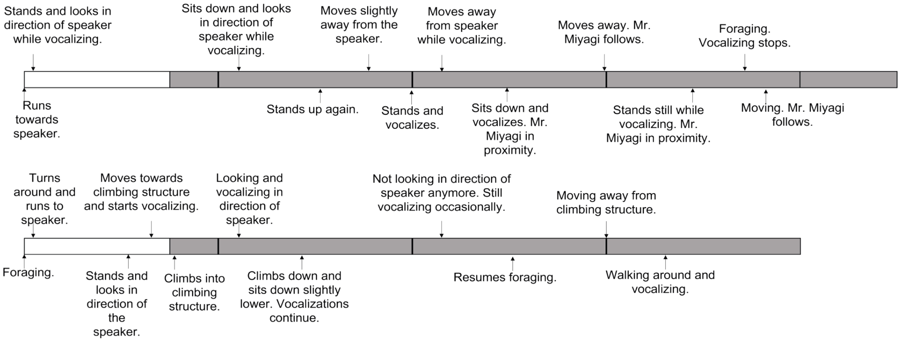


Figure 2. Description of the behavioural responses of Temmy to the long call stimuli on day 1 of the first study period. The white bar represents the duration of the stimulus playback, while the shaded bar represents the post-stimulus period. The area between two thick black lines represent one minute.

Study period 2

66 days after the first study period, we returned to Allwetter Zoo, and played a few more long call recordings and control sounds to Temmy while she was -most likely- not ovulating. If her strong behavioural responses were the result of a novel sound, and the relaxation of her response over time the result of habituation, we would expect to see a strong response to the long call stimuli after 66 days of no exposure to the stimuli. If the behavioural responses were caused by ovulation, however, we would expect to see no noticeable response during the second study period.

The results from the second study period match with the latter: Temmy did not show the strong behavioural response that she showed during the first study period. In total, we played her seven long call stimuli and five control stimuli in two days. The only noticeable response to the stimuli was that Temmy sometimes looked towards the speaker while the stimulus was played, but she did not vocalise or walk towards the source of the stimuli as she had done at the beginning of study period 1.

Eloise

Our second case concerns Eloise, a Bornean orang-utan female living in LA Zoo. To our understanding, she had been producing vocalisations during ovulation since she became of reproductive age. Although no consistent records exists with regard to this specific behaviour at earlier stages of her life, one of the authors (MF) has worked as her main caregiver since 1999, and observed that she consistently produced vocalisations during ovulation until approximately 2018. The vocalisations consistently co-occurred with ovulation, as evidenced by the fact that Eloise consistently produced the vocalisations approximately two weeks after onset of her menstruation on a monthly basis. Furthermore, her vocalisations coincided perfectly with increased proceptivity towards the flanged male that she was housed with, reflected in following the male and actively soliciting him.

During ovulation, Eloise would actively pursue the male, while outside of her ovulation timeframe she would not actively seek him out. This would include her following him throughout the exhibit space; when he would move areas, she would actively follow. She would also position herself for copulation, trying to solicit a response from the male. The male would copulate with Eloise, and would occasionally want to be housed with her overnight. Given Eloise's condition, she was subordinate to the other females in the group. If any of the other females were ovulating at the same time as Eloise, she would be supplanted and pushed away by the females. Otherwise, these females would not intervene. Her ovulation lasted approximately 3-4 days, with the vocalizations being most intense during the first day or two of the cycle and slowly tapering off.

The fact that her vocalisations started 2 weeks after her menstruation, and coincided with an increase in proceptivity as well, suggests that the vocalisations were induced by ovulation. This conclusion is further supported by the fact that disappearance of the vocalisations co-occurred with Eloise's transition towards her post-reproductive period. Thus, when Eloise's menstrual cycle became less regular, her calls became less frequent and eventually disappeared.

Vocalisation analysis

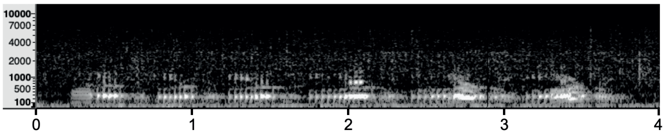
During all playbacks that we performed in the period of study 1 for which we suspect Temmy was in the peri-ovulatory period, Temmy performed vocalisations. We were able to capture three good quality recordings of the vocalisation that Temmy produced. These calls consisted of short series of 5 to 6 consecutive bark-like vocalisations (hereafter pulses; Figure 3). Each call lasted on average 4.2 seconds (SD=0.3), in the longest recording these calls were repeated consecutively for more than 3 minutes. Each bark-like pulse within the call had an average duration of 690ms long (SD=48ms), with an average fundamental frequency of 250 Hz. These parameters remained consistent across all of Temmy's vocalisations. Only the intensity of the calls decreased sharply after 65 seconds of vocalising. Still, the softer calls remained similar in the other acoustic parameters.

Interestingly, the calls that Temmy emitted in response to the playbacks seem to be different from any calls generally known to be uttered by orang-utans. To validate this, we compared Temmy's calls to known sounds in the orang-utan repertoire: the grumble, complex call, rolling call, gorkum and lork call. These comparisons were based on 4 main features, call duration (s), peak frequency (Hz), fundamental frequency (Hz) and inter-onset-interval length (s) (Figure 3). The complex call, rolling call and gorkum all have one high frequency burst in the 3500 Hz range, something that is missing from Temmy's vocalisations during the playbacks. However, based on the temporal structure, these calls are rather similar. Temmy's vocalisations might be a variation on the complex call that lacks the high burst and where the emphasis is mainly on the low-frequency grunts. Based on the frequency range, there is more similarity with the grumble, a call with a quick repetition of short and low pulses. These same pulses seem to occur in Temmy's vocalisations. However, Temmy's are higher in frequency (250 instead of 150 Hz) and occur in more tightly knitted sets. The lork call seems to be most similar to Temmy's vocalisations. Both are relatively long calls (>60 seconds) with low frequency pulses. Nevertheless, the lork calls are much slower than Temmy's vocalisations. Both the separate pulses as well as the pauses between these pulses are about double the length in the lork calls than in Temmy's vocalisations. This means that these vocalisations of Temmy in response to the male long-call share features of some of the known calls from the orang-utan repertoire but bear no complete similarity to any of them.

Temmy's vocalisations seem to be most similar to the long-calls of male orang-utans (Figure 4). Male long calls also consist of bark-like pulses that average around 800ms each (average IOI of 1.5 sec) with a fundamental frequency of around 320 Hz. An analysis of the spectral information also shows that most of the power in these calls occurs in the same spectrum, between 200 and 350 Hz, with little to no power in the higher frequencies. With regard to the temporal structure, these calls bear strong resemblance in the sound onset timing. In addition, the duration of each pulse is similar between Temmy's vocalisations and male long-calls. Temmy's pulses have inter-onset-intervals (IOIs) of approximately 740ms (SD=61ms), whilst the 12 male long calls that we analysed have IOIs of approximately 800ms (SD=54ms). The clearest difference between Temmy's vocalisations and the male long-calls lies in the overall temporal structure. Long-calls consist of rather regular repetitions of pulses that can last up to 3 minutes with steady IOIs. Temmy's calls could also last up until 3 minutes in total, but with concatenations of bouts of 5-6 pulses, followed by a longer pause (+/- 2,5 sec.) before there was another pulse-bout. The IOIs within these bouts are similar to male long-calls, but the pauses between bouts are not typical for long-calls. To conclude, Temmy's call seems to be most similar in temporal structure and frequency distribution to the male long-calls and less so to other orang-utan vocalisations.

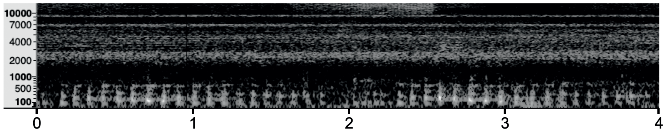
A second female, Eloise, proactively produced calls that also bear similarities with male long calls. Rather than the reactive calls of Temmy to long-call playbacks, this female produced long-call-like calls spontaneously. Eloise's calls mainly differ from Temmy's with respect to timing. Each pulse is much longer, with an average of 2.237 sec per pulse (average IOI 2.467 sec.). This makes her pulses also longer than those of the male long-call. However, unlike the concatenated pulse-bouts in Temmy's calls, Eloise's full calls retained a regular IOI pattern for

a. **Temmy's response**



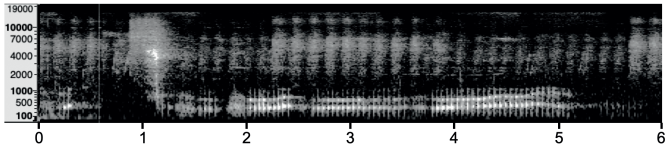
Call duration: 3,8 sec
Peak frequency: 940 Hz
Fundamental freq: 250 Hz
IOI length: 720 msec

b. Grumble



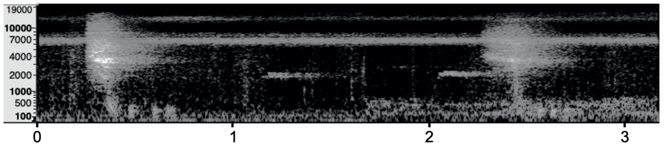
Call duration: 3,5 sec
Peak frequency: 124 Hz
Fundamental freq: 124 Hz
IOI length: 1,9 sec

c. Complex call



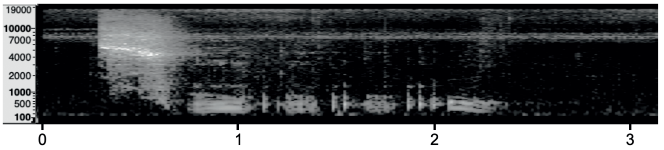
Call duration: 4,5 sec
Peak frequency: 4042 Hz
Fundamental freq: 259 Hz
IOI length: 5,3 sec

d. Rolling call



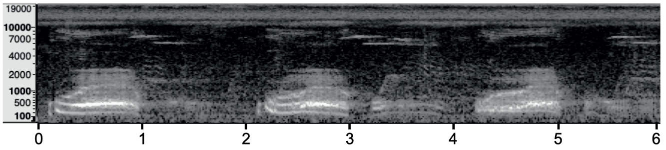
Call duration: 2,9 sec
Peak frequency: 3356 Hz
Fundamental freq: 1899 Hz
IOI length: 1,9 sec

e. Gorkum



Call duration: 3,5 sec
Peak frequency: 4303 Hz
Fundamental freq: 2220 Hz
IOI length: 1,2 sec

f. Lork Call

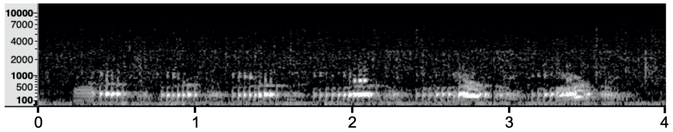


Call duration: 103 sec
Peak frequency: 366 Hz
Fundamental freq: 172 Hz
IOI length: 2,6 sec

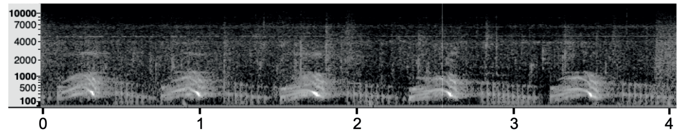
Figure 3. Comparison between Temmy's vocal response to other vocalisations known in the orang-utan repertoire. Analysed aspects of the vocalisations were: total call duration (s), Peak frequency (loudest frequency of the call), fundamental frequency (lowest frequency of the call), Inter-onset-interval (time between start of one vocalisation to start of next vocalisation within the call). B-f indicate 5 different orangutan calls that bear certain similarities to Temmy's vocal response. Neither of them can be categorized as the same call that Temmy is producing.

the whole duration. One call could continue for up to 60 seconds with steady IOIs, which bears more similarity to the long stable duration of the long-calls which generally last between 60 and 120 seconds. With respect to the fundamental and peak frequency, Eloise's calls were closer to the male long call compared to Temmy's (average Eloise fundamental frequency: 300 Hz, male long-call around 350 Hz, Figure 5).

a. Temmy's response



b. Male long-call

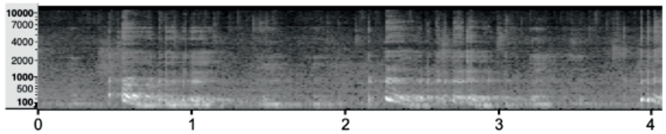


Call duration: 93 sec
Peak frequency: 1240 Hz
Fundamental freq: 350 Hz
IOI length: 1.5 sec

Figure 4. Male long-call spectrogram in comparison with Temmy's vocal response. Male long-calls have a longer total duration than Temmy's vocalisations, but the pulses bear many resemblances in spectral and temporal pattern.

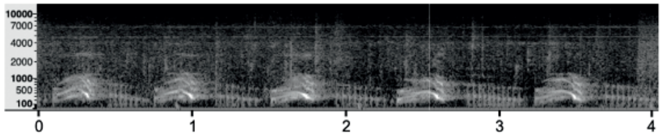
In comparison to the known repertoire of orang-utans, it is noticeable that these calls bear less resemblance to these known vocalisations. It might come closest to the complex call which has also relatively long and low call units. However, the units in the complex call are produced as several short, consecutive bursts, whilst the long-call-like call of Eloise is one long burst on an exhale, followed by an audible inhale. Especially the long duration of the pulses and the total call duration of Eloise's vocalisations make them incomparable to any of the known orangutan calls.

a. Eloise's response



Call duration: 59 sec
Peak frequency: 1123 Hz
Fundamental freq: 300 Hz
IOI length: 2.4 sec

b. Male long-call



Call duration: 93 sec
Peak frequency: 1240 Hz
Fundamental freq: 350 Hz
IOI length: 1.5 sec

Figure 5. Eloise's vocalizations in comparison to the male long-call. The pulses in Eloise's call are longer than those of the male-long call. However, the overall call structure and total call length are similar. The spectral information of the call also bears many similarities to the male long-call.

Discussion

In this anecdotal report, we describe two cases of ovulation-induced proceptivity and vocalisation in zoo-housed Bornean orang-utans. First, we described the case of Temmy, who was likely ovulating when we opportunistically played long call recordings to her. She showed a strong bodily and vocal response to these calls, but her response disappeared after two days. A follow-up experiment suggests that her change in response did not seem to be driven by habituation. Second, we described the case of Eloise, a female who consistently produced specific vocalisations during ovulation, paired with increased proceptivity towards the male she was housed with. When she reached post-reproductive age, she ceased producing this vocalisation. Even though we want to emphasize that anecdotal reports should be interpreted with caution (Sándor & Miklósi, 2020), our report suggests that changes in orang-utan female's behaviour and vocal repertoire might reflect proceptivity during ovulation. Below, we discuss possible implications for our understanding of the role of female orang-utan behaviour in facilitating mating in captivity and in the wild.

As mentioned in the introduction, previous studies have described that orang-utan females show changes in proceptivity across their menstrual cycle. Our results further substantiate this pattern. We observed how Temmy responded very strongly to male long calls during her ovulation. She actively approached the source of the sound, while she did not do this during control trials. Furthermore, this behaviour was not observed outside of her peri-ovulatory period. Her behavioural response seems to suggest male-seeking behaviour, which would be especially relevant for a semi-solitary species like Bornean orang-utans. Such ovulation-dependent male-seeking behaviour has previously been described in other mammal species (rats, *Rattus norvegicus*: Nofrey et al., 2008; sheep, *Ovis ammon*: Sutton & Alexander, 2019). More specifically, in some primate species females actively seek proximity with males during ovulation (reviewed in Dixson, 2012). Our observations of Temmy suggest male long calls might induce male-seeking behaviour in ovulating orang-utan females, which could results in proximity with preferred flanged males. Some studies on wild orang-utans provide indirect evidence for this: Sumatran orang-utan females seem to approach long calls irrespective of their reproductive state (Mitra Setia & van Schaik, 2007), while in Bornean orang-utans only sexually active females without dependent infants approached long calls (Spillmann et al., 2010). However, these studies did not account for ovulatory status. Therefore, it remains to be established whether wild orang-utan females indeed show a stronger approach tendency during ovulation, like Temmy did. Nevertheless, Knott et al. (2009) suggest that ovulating females show an increase in encounters with in flanged males, resulting in more copulating events with them. Thus, male long calls might be an important stimulus that guides ovulating females towards preferred flanged males, and future studies can further elucidate the mate attraction function of long calls by comparing female responses to male long calls at different points during their menstrual cycle.

Eloise's case supports the notion that ovulating orang-utan females have an important role in facilitating mating. In the period that we described, Eloise showed proceptive behaviour in the form of following the male and actively soliciting him. This is in line with results from restricted-access tests (Maple et al., 1979; Nadler, 1995): when orang-utan males have free access to females, mating events are quite evenly spread across the menstrual cycle. However, when females can control access, they specifically approach males during ovulation. This is also supported by the fact that wild orang-utan females selectively mate with flanged males during their peri-ovulatory period (Knott et al., 2009). Thus, it might be the case that matings are mostly characterised by receptivity outside the peri-ovulatory period (Durgavich et al., 2023), while they are characterised by increased proceptivity followed by receptivity during the peri-ovulatory period. These proceptive behaviours could include actively approaching long calls, following males, and soliciting. In addition, ovulation-induced vocalisations could be considered proceptive behaviours.

Up until now, relatively few vocalisations have been described that are unique to orang-utan females (Hardus et al., 2008). Two of these unique vocalisations occur in the context of mating, namely the mating squeal and the fear squeal. However, to our knowledge, there are no descriptions of female ovulation calls. In this report, we described two seemingly new vocalisations that could possibly be considered ovulation calls. Both Temmy and Eloise produced vocalisations that showed resemblances in spectral and temporal pattern to the male long call. However, Temmy's vocalisations seemed to travel a relatively short distance, while Eloise's vocalisations seem much louder, and could be considered middle- or even long-distance calls (*sensu* Hardus et al., 2008). As far as we know, only one other female long-distance vocalisation has been described for orang-utans, namely the *lork call* (Hardus et al., 2008). According to Rijksen (1978) this call might function as an advertisement call, or as an expression of agonistic state.

However, both Temmy's and Eloise's vocalisations seem to differ from the lork call in several aspects. Altogether, our observations suggest that orang-utan females might have a more extensive vocal repertoire that has been assumed.

While we want to be careful to ascribe a function to the vocalisations, we do think it is interesting to provide suggestions. The most likely function of the calls would be mate attraction. Especially for relatively solitary animals like orang-utans, it might be essential to coordinate movement. Long calls have such a coordinative function (Delgado et al., 2008; Mitani, 1985), but it could well be that female vocalisations also contribute. Although proceptive vocalisations seem to be rare in primates (Dixson, 2012), females of at least two other relatively solitary primate species seem to produce proceptive vocalisations that can travel relatively long distances (grey mouse lemur, *Microcebus murinus*: Buesching et al., 1998; aye-aye, *Daubentonia madagascariensis*: Sterling & Richard, 1995). Given that Eloise's vocalisation was relatively loud, the mate attraction hypothesis would be a likely candidate to explain her vocalisations. However, Temmy's call seems to travel relatively short distance. Potentially, short-distance vocalisations like Temmy's communicate mating motivation or induce arousal in males. Such vocalisations have also been described in other primate species (Dixson, 2012). For example, gelada (*Theropithecus gelada*) females produce pre-copulatory vocalisations, especially during ovulation (Roberts et al., 2017). The length of these calls is a predictor of copulation duration (Zanoli et al., 2022), suggesting that these calls are an indicator of female sexual motivation. Thus, female proceptive vocalisations have previously been described in other primate species, and are potentially present in orang-utans.

It is important to note, though, that these functional accounts are also in conflict with an important aspect of orang-utan sexuality, namely concealed ovulation in females. Orang-utan females show no outward indicators of ovulation (Knott & Kahlenberg, 2011). It has been suggested that concealment of ovulation reduces infanticide risk through paternity confusion (Kunz et al., 2022). If concealing ovulation is indeed beneficial for females, ovulation-induced vocalisations could be detrimental. Therefore, it is also possible that ovulation-induced vocalisations have negative fitness consequences, which would explain why such vocalisations have not previously been described in wild orang-utans. Our cases concern two females from the zoo-housed population, and such housing is often associated with changes in selective pressures (Williams & Hoffman, 2009). Specifically, orang-utan females are often housed with only one breeding male in zoos, which might reduce the likelihood of infanticide, while wild orang-utan females need to navigate a more complex social environment, with multiple males that might pose a threat. Thus, while ovulation-induced vocalisations might occasionally be observed in zoo-housed females, they might be under strong negative selection in wild orang-utan populations due to increased risk of infanticide for females who produce such vocalisations.

Studying mating behaviour of orang-utans in the wild is particularly challenging for multiple reasons (Durgavich et al., 2023). First, they are predominantly solitary, which means that only one individual can be observed at a time. Second, individuals often travel outside of the study area or disappear out of the view of the observers, making it difficult to follow the same individual for prolonged periods. Third, the menstrual cycle of orang-utan females is often suppressed, either because they are pregnant, lactating, or have a negative energy balance. Fourth, if a female is cycling, it is difficult to determine whether she is ovulating: there are no clear morphological indicators, and obtaining urine samples from arboreal species can be difficult. In captivity, researchers are confronted with fewer of these limitations. Thus, studies in captivity can prepare us to conduct methodical observations by describing relatively rare behaviours that may nonetheless occur in the wild.

In conclusion, we described two cases of increased proceptivity during ovulation in two zoo-housed Bornean orang-utan females. Both females also produced vocalisations during their peri-ovulatory period. In the case of Eloise, she produced such vocalisations during her ovulation consistently, for multiple years. We want to emphasise that we cannot ascribe a clear function to the vocalisations, given that our report is anecdotal (Sándor & Miklósi, 2020). Nevertheless, our observations open up possibilities that the orang-utan female vocal repertoire might include vocalisations that indicate proceptivity, and might thus be more extensive than previously thought, at least in captivity. However, it remains to be established whether such vocalisations also occur in wild orang-utan females.

Chapter 9

General discussion

Primates, including humans, often rely on visually conspicuous traits to judge the quality of a potential mate (Petersen & Higham, 2020; Rhodes, 2006). Because choosing a good-quality mate has a significant bearing on an individual's biological fitness, it has been suggested that such traits have a strong influence on the cognitive processes of humans (Maner & Ackerman, 2015) and other animals (Bateson & Healy, 2005). Consequently, Maner & Ackerman (2015) proposed the term *sexually selective cognition* for cognitive attunements and biases related to mate choice. However, to date, sexually selective cognition has almost exclusively been studied in humans, whereas systematic studies in non-human primates are rare. This is unfortunate because a more comparative approach would allow for a better understanding of the phylogenetic history of sexually selective cognition. Moreover, this understanding can have practical implications for the management of primate populations in zoos.

This thesis addresses this fundamental research gap by investigating the interplay between cognition and mate choice in humans and Bornean orang-utans (*Pongo pygmaeus*) while simultaneously considering practical implementations within zoo breeding programmes. More specifically, I investigated whether humans and Bornean orang-utans show similar cognitive biases for mate-relevant information when presented with similar tasks, with an emphasis on attentional biases. I begin by summarizing the main findings of each chapter. The primary objective of the chapter summary is to offer a succinct overview of the main discoveries in each chapter, without integrating the results across chapters or with the existing body of literature. Following this, the subsequent sections will integrate the findings from various chapters and compare them to the existing literature, encompassing theoretical implications, methodological considerations, and practical implications. Finally, the chapter will conclude with a comprehensive summary.

Summary of main findings

In **Chapter 2,** I reviewed the literature on sexually selective cognition in humans and non-human primates. While a plethora of methods have been employed to investigate the interplay between attractiveness and cognition in humans, encompassing attentional processes, memory, and motivational processing, relatively few studies have investigated this phenomenon in non-human primates. Moreover, the few studies that have investigated the link between attractiveness and cognition have mainly focused on visual attention, employing a preferential looking paradigm, even though a wide range of test paradigms has been developed to study primate cognition in recent decades. To close this gap, I suggested test paradigms that can be used across species to study sexually selective cognition from a comparative perspective. Furthermore, I discussed how these paradigms can be applied to investigate partner preferences in conservation breeding programmes, which may benefit well-being of captive animals and increase their reproductive success.

Primates are characterised by visual specialisation (Barton, 1998; DeCasien & Higham, 2019), and thus studies investigating sexually selected traits tend to focus on conspicuous visual traits (e.g., Petersen & Higham, 2020; Rhodes, 2006). Nevertheless, it has been suggested that research on human attractiveness should also embrace olfactory and auditory attractiveness, as voices and smells can convey a large amount of information about a person (Groyecka et al., 2017). In **Chapter 3,** I therefore investigated the unique role of visual, auditory, and olfactory attractiveness in human mate choice by combining multimodal attractiveness rating tasks with speed-dating, an ecologically valid paradigm to study human mate choice (Finkel & Eastwick, 2008). Sixty-seven heterosexual adolescents participated in the experiment, resulting in a total of 277 speed dates. The results indicate a strong positive link between idiosyncratic ratings of visual attractiveness before the date and the willingness to date again after the date. However, I found only equivocal effects for the idiosyncratic auditory and olfactory ratings. These findings provide strong evidence for the notion that attractiveness is especially in the *eye* of the beholder. That is, mainly visual information influences whether we perceive conspecifics as attractive or not. This is in line with a plethora of previous studies.

In **Chapter 4,** I investigated how general ratings of facial attractiveness or variation in attractive traits modulate implicit cognition in humans. Zoo visitors (*N* = 450 across the three experiments) participated in a dot-probe task (MacLeod et al., 1986) with stimuli varying in attractiveness category, a dot-probe task with stimuli varying in facial symmetry, or a gaze cueing task (Deaner et al., 2007) with stimuli varying in attractiveness category. The stimuli were obtained from a large standardized dataset (Ma, Correll, et al., 2015). In Experiment 1, I presented participants with attractive or unattractive faces paired with intermediately attractive faces. In line with our expectations, the implicit attention of participants was drawn to attractive but away from unattractive faces. In Experiment 2, I presented participants with faces that varied in symmetry, a trait often considered to be correlated with facial attractiveness. Contrary to our expectations, I found no robust effect of facial symmetry on implicit attention. In Experiment 3, I employed a gaze-cueing paradigm (Deaner et al., 2007) to investigate whether participants would more readily follow the gaze of attractive faces. While I found a strong gaze cueing effect, this effect did not vary according to attractiveness category. Furthermore, I found no evidence of age or sex effects in either of the experiments. The findings presented in this chapter suggest that implicit attention but not gaze cueing is modulated by attractiveness. In addition, this attentional bias was present across age groups, and in both male and female participants. Previous studies on implicit attention have incorporated only attractive and intermediately attractive stimuli, and could not therefore investigate the differential effects of attractive and unattractive stimuli on implicit attention. Our findings showed that attention was specifically drawn to attractive faces but not to unattractive faces. This suggests that the attentional bias is not solely driven by the deviation of attractive faces from the average face, as unattractive faces also deviate from the average face but do not receive preferential attention.

In Chapter 4, I defined attractiveness categories based on previous ratings by an independent group of raters. Although humans strongly agree on attractiveness ratings (Langlois et al., 2000), 50% of the variation can be explained by individual preferences (e.g., Hönekopp, 2006). Therefore, **Chapter 5** examined the relationship between idiosyncratic attractiveness preferences and visual attention in a realistic mate choice context. I combined visual attractiveness rating tasks with two well-established attentional paradigms: a dot-probe paradigm to investigate immediate attention, and a preferential looking paradigm to investigate voluntary attention. Furthermore, all participants went on speed dates after completing the tasks. In line with previous studies, I found considerable inter-rater variability in the attractiveness ratings. With regard to immediate attention, idiosyncratic ratings of visual attractiveness were a good predictor of immediate attention in males, but not in females (*N* = 57 participants), although I found no robust sex effect. However, both male and female participants (*N* = 35 participants) showed a strong bias towards attractive faces in the preferential looking paradigm. Moreover, I found no consistent relationship between speed date outcome and immediate attention (*N* = 56 participants), whereas I found a robust association between speed-date outcome and voluntary attention for both male and female participants (*N* = 35 participants). Our results complement previous studies that have found an association between general attractiveness ratings on attention (Ma, Zhao, et al., 2015; Roth et al., 2022) by showing that the same applies for idiosyncratic attractiveness ratings. Furthermore, our findings suggest that biases in voluntary attention concord with mate choice.

In **Chapter 6**, I moved away from humans and focused on Bornean orang-utans (*Pongo pygmaeus*). Across three touchscreen experiments, I investigated whether Bornean orang-utans showed an implicit attentional bias towards males with larger flanges or more symmetrical faces using the dot-probe paradigm. Furthermore, I presented orang-utans with a choice task that allowed them to view a picture of either a flanged or unflanged male. Previous studies have suggested that orang-utan females prefer to mate with flanged males (Knott et al., 2009). Furthermore, facial symmetry has been linked to health in multiple primate species (Little et al., 2012; Sefcek & King, 2007). Therefore, I expected individuals to immediately attend to males with larger flanges and symmetrical faces and to choose to look at flanged males. However, none of our expectations were confirmed: individuals had no clear attentional biases in the dot-probe paradigm and chose to look at flanged and unflanged males equally often in the choice task. Furthermore, the pattern in which they selected flanged and unflanged stimuli seemed random, as I did not find evidence for temporal clustering. However, I did find evidence for energy efficiency trade-offs and a colour bias in the preference task. The findings of this chapter cast doubt on the suitability of extrinsically rewarded touchscreen experiments to test partner preferences of zoo-housed orang-utans.

In **Chapter 7**, I employed non-invasive eye-tracking to investigate immediate and voluntary attention in Bornean orang-utans across two experiments. To this effect, I presented individuals (*N* = 4) with two stimuli that were presented simultaneously for four seconds. In Experiment 1, these presentations always consisted of one flanged and one unflanged male. In Experiment 2, I also presented pairs consisting of two flanged or two unflanged stimuli. Across the two experiments, I found that orang-utans (1) were more likely to fixate first on stimuli of flanged males, and (2) spent a larger proportion of time looking at flanged males. Furthermore, I found some indications of individual preferences in Experiment 2. Taken together, our results suggest that orang-utan attention is attuned toward flanged males, which suggests that sexual selection shaped attentional processes in orang-utans. However, our results should mainly be considered at the proximate level, as I cannot explain *why* orang-utans specifically attended to flanged males. Their attentional bias might be driven by positive-valenced interest, but could also be the result of vigilance. This is also reflected in the fact that the participating male also had a bias towards flanged male stimuli. Therefore, future studies should further investigate the motivational drives behind this attentional bias.

While Chapters 6 and 7 focused on visual processing, **Chapter 8** reports the link between auditory signals and sociosexual behaviour of Bornean orang-utans. Because orang-utans are characterised by a dispersed social system, vocalisations might be crucial for social organisation and reproductive strategies (Delgado, 2006). I report anecdotal evidence of two zoo-housed Bornean orang-utan females which supports this idea. First, I described the behavioural response of Temmy to male long-call playbacks while she was ovulating. She showed a strong tendency to approach the origin of the sound, whereas she did not do so when I played control sounds. Furthermore, she responded by producing vocalisations. Second, I described the case of Eloise, who consistently showed an increase in proceptive behaviour during ovulation for at least over a decade. Similar to Temmy, she produced vocalisations during her ovulation. However, in contrast to Temmy, she proactively produced them. Both the vocalisations produced by Temmy and Eloise seem distinct from previously described orang-utan vocalisations. Thus, these observations suggest that the female vocal repertoire may be more extensive than previously thought. While conclusions about the function of these calls remain tentative, they may facilitate coordination between ovulating females and flanged males.

Overall, this thesis has shown that (1) sexually selective cognition has rarely been studied in non-human primates, even though suitable test paradigms are available, (2) human initial mate choice is strongly determined by visual attractiveness, and not auditory or olfactory attractiveness, (3) human attentional processes are attuned to visual attractiveness, both when using general ratings and idiosyncratic ratings of attractiveness, (4) Bornean orang-utans have an attentional bias in immediate and voluntary attention towards flanged males in an eye-tracking task, but no attentional biases or choice biases towards male flanges and/or facial symmetry in touchscreen tasks, and (5) Bornean orang-utan females can show both a behavioural and vocal response to visual or vocal indicators of flanged male presence during ovulation. Although these results have relevant theoretical and practical implications, methodological considerations and important knowledge gaps remain. This is discussed in the following section.

Theoretical implications

The multimodality of attraction

Human mate choice can be considered a two-stage process, consisting of two main filters (Dixson, 2012). While the first filter is thought to mainly focus on physical traits and attractiveness (attraction: Fisher, 1998), the second filter is more closely associated with personality traits and behavioural coordination (attachment: Fisher, 1998). In this thesis, I have specifically focused on the first filter, because *sexually selective cognition* is especially relevant at this point in time. Dixson (2012) postulates that the first filter consists of multimodal perception of attractiveness, encompassing olfactory, auditory and visual information. This is also in line with a recent paper that argued for a stronger integration of olfactory and auditory attractiveness in the study of human mate choice (Groyecka et al., 2017). However, the results of Chapter 3 strongly suggest that such a shift of focus is premature, at least in the context of initial mate choice. In contrast with the notion that multimodal attractiveness is important in human mate choice, I found strong evidence only for the role of visual attractiveness in initial mate choice, whereas attractiveness of smell and voice seemed to have little to no bearing on speed-date outcome.

This is not to say that olfactory and auditory information do not play a role in human mate choice at all. More specifically, these modalities could be especially relevant in early stages of inter-personal contact where auditory and olfactory information can be reliably perceived and evaluated, such as contexts in which no other people are present. However, during initial interactions this will often not be the case, and visual information may be the most reliable source of information in such a context. Therefore, I suggest splitting Dixson's (2012) attraction filter into two parts (Figure 1): potential mates are first discriminated based on visual attractiveness, because this is often the most conspicuous and reliable source of information. In the second attraction filter, auditory and olfactory information would play a larger role. Importantly, this filter could be applied simultaneously with the attachment filter. Furthermore, there might be trade-offs between the different filters, to the extent that 'scoring high' on one filter may to some extent compensate for 'lower scores' on another filter (Figure 1). However, these trade-offs require further investigation. A further point that requires attention is the link between culture and mate choice for odour. The effect of olfaction on mate choice could very well vary between cultures due to cultural variation in the use of hygienic products and fragrances and attitudes towards natural body odour (Ferdenzi et al., 2020). However, recent work shows that variation in odour awareness is not well-explained by cultural differences, which suggests that there might be large individual differences in the importance of body odour for mate choice irrespective of culture (Sorokowska et al., 2018). In short, while multimodal perception of attraction might be at work during the early stages of inter-personal contact, my work suggests that existing models are not specific enough and require more finetuning.

In addition, Chapter 4 and 5 provide evidence for the notion that biases in attention are associated with this first attraction filter. This is in line with the idea that evolutionary relevant stimuli should receive preferential attention (Cosmides & Tooby, 2013). In Chapter 4 I have shown that an immediate bias towards generally attractive faces is present in a wide community sample, irrespective of sex and age of the perceiver. The results of Chapter 5 are somewhat in contrast with this result. More specifically, when testing adolescents that were motivated to find a partner, only men showed a robust immediate attentional bias towards more attractive opposite-sex stimuli. When considering voluntary attention, however, I identified a strong attentional bias towards attractive opposite-sex stimuli in both men and women. The results with regard to immediate attention are somewhat unexpected, because the attentional biases reported in Chapter 4 and 5 are very similar in effect size despite the fact that participants in Chapter 4 cover a wide age range and might have been in a relationship already, whereas the participants in Chapter 5 were all single and motivated to find a partner. This is in contrast with motivational approaches to cognition (Kenrick et al., 2010; Schaller et al., 2017), that suggest that motivational states bias cognitive processes in a functional way towards motivationally salient information. If that would be the case, one would have expected participants in the speed-date study to show a stronger attentional bias towards opposite-sex stimuli than participants from the community sample, because participants in the speed-date study were motivated to look for a partner. Thus, the findings of this thesis seem to point more towards a domain-general mechanism underlying bias towards attractive faces than a domain-specific mechanism that becomes only apparent in the context of mate choice (Principe & Langlois, 2012; Trujillo et al., 2014).

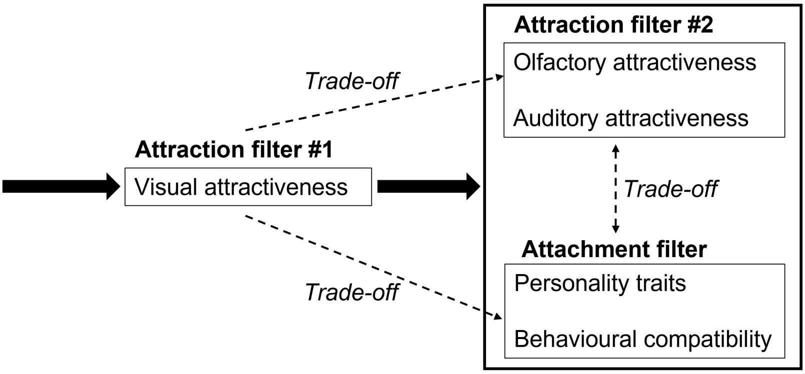


Figure 1. Schematic depiction of the updated two-stage modal of human mate choice. The model still consists of two stages. However, stage two now consists of two separate filters. Furthermore, the model explicitly mentions trade-offs between different filters, allowing for a high 'score' on one filter to compensate for a lower 'score' on another.

The link between cognitive bias and behaviour

In addition, the results from Chapter 4 cast doubt on the link between attractive *traits* and immediate attentional biases. Whereas people did immediately attend to attractive faces, they did not show evidence of differential attention as a function of facial symmetry. This could be interpreted in two main ways. First, it could be argued that sexually selective cognition concerns attunement towards holistically attractive faces, and not specifically to slight variations in features that contribute to attractiveness. Second, it can be argued that facial symmetry is not as important for mate choice as has been argued in the past (e.g., Thornhill & Gangestad, 1999), and therefore does not receive preferential attention. The first interpretation cannot be rejected at the time of writing, because no cueing studies have been performed that use faces that vary in attractive traits other than symmetry, such as facial averageness or sexual dimorphism. The second interpretation, however, seems to concord with recent literature in multiple aspects. First, data-driven approaches to facial attractiveness have recently shown that facial symmetry does not contribute to attractiveness ratings (Holzleitner et al., 2019; Jones & Jaeger, 2019). Second, the link between mate quality and facial symmetry is heavily debated, given the lack of correlation between measures of health and facial symmetry (e.g., Foo et al., 2017; Pound et al., 2014). The results of Chapter 4 corroborate this interpretation, although it is not yet clear whether people show biases in immediate attention towards other traits that are linked to attractiveness, such as facial averageness.

One important assumption that underlies evolutionary approaches to cognition, is that cognitive adaptations or biases also translate into behavioural differentiation (Cosmides & Tooby, 1992). For example, attentional sensitivity to threats in the environment can guide avoidance behaviour, and thereby increase an individual's fitness. Such a link has not been established yet in the context of sexually selective cognition. However, Chapter 5 suggests that a link between attentional biases may exist. While many studies have investigated the interplay between cognition and attractiveness, very few studies have linked cognition to real-world mate choice. Admittedly, many studies have established a link between attentional processes and sexual behaviour, to the extent that heterosexual and homosexual participants show differential attention towards same- and opposite-sex stimuli (Dawson & Chivers, 2016, 2018). In addition, with regard to other topics, evidence suggests a strong link between substance abuse and attentional biases towards these substances (Field & Cox, 2008; Sharbanee et al., 2013; Weafer & Fillmore, 2013), suggesting a direct link between attentional biases and behaviours. However, these attentional biases all relate to general perceiver behaviour, and not specifically to an interactive effect of perceiver and stimulus on behaviour. Nevertheless, if sexually selective cognition would indeed aid people to identify suitable mates, a link between cognitive measures and valid measures of mate choice need to be firmly established. Recently, it has been established that initial impressions have a lasting effect on long-term mate choice in humans (Baxter et al., 2022), and functional cognitive biases potentially play a role in this. Accordingly, the results of Chapter 5 of this thesis are a first attempt to establish a link between attentional biases to preferred mates and mate choice based on speed-dates. Future work could try to further explore this line of research by combining cognitive tasks and speed-dating in order to get a better insight into the link between cognitive biases and mate choice. Such knowledge is essential to understand the role of cognitive processes in the first attraction filter.

The attraction filter in regard to orang-utan mate choice

With regard to this filter, it still has to be established whether such a multi-stage model applies to non-human primates as well, and whether they possess sexually selective cognition. In Chapter 1, I suggested that orang-utans very likely only possess an attraction-filter, because they do not form long-term pair bonds. If they indeed possess such a filter, the most likely visual traits that would be "filtered", would be traits of fully developed flanged males, such as large cheek pads on the side of the face. Therefore, I investigated whether Bornean orang-utan cognition would be biased towards stimuli depicting males bearing this trait. However, the results are mixed, with no evidence of cognitive attunement towards flanged males in Chapter 6, but evidence of immediate and voluntary attentional bias towards flanged males in Chapter 7. The eye-tracking results from Chapter 7 do indeed suggest that orang-utan cognition is attuned towards flanged males. This corroborates previous work in rhesus macaques, where systematic studies have established links between visual attention and visually conspicuous traits, such as facial masculinity (Rosenfield et al., 2019), facial coloration (Dubuc et al., 2016; Waitt et al., 2003), and facial symmetry (Waitt & Little, 2006). Thus, attentional biases towards conspicuous facial traits that are thought to play a role in mate choice seem not to be restricted to rhesus macaques, but might be more widespread across primate species, including great apes. It is important to note, though, that the results of Chapter 6 do not provide evidence for the notion that orang-utan cognition is biased towards flanged males. However, I will further elaborate on this in the section “Methodological considerations”.

Furthermore, Chapter 8 suggests that the first filter of orang-utans might also be sensitive to auditory information. From a functional cognition perspective, this would make sense, as orang-utans are considered semi-solitary (Roth et al., 2020; van Schaik, 1999). Because of their dispersed social system, auditory communication has a pivotal role in inter-individual coordination (Delgado, 2006). Consequently, orang-utan females will often have access to auditory information from males, but not visual information. Therefore, auditory information may have an important role in female orang-utan mate choice. While some evidence for this has been found in Sumatran orang-utans (Mitra Setia & van Schaik, 2007), results for Bornean orang-utans do not support this notion (Mitani, 1985; Spillmann et al., 2010). Nevertheless, this point underlines the need for a biocentric approach to animal cognition (Bräuer et al., 2020). While presenting identical tasks to different species may seem an objective approach to comparative cognition, this approach ignores the fact that each species has its uniquely adapted sensory systems. Therefore, it is crucial to consider the specific sensory modalities and environmental contexts of each species when studying animal cognition.

Caveats in interpreting the results of cognitive bias tasks

Thus, it is possible that orang-utans indeed possess an attraction-filter, and that sexually selective cognition is one of the mechanisms through which this filter functions. However, I want to mention three caveats. First, the eye-tracking results cannot be considered evidence for an attentional bias that is driven by *positive evaluation*. It could also be the result of *vigilance* towards flanged males, because they can be a threat to both males, with whom they may compete, and females and their offspring. Therefore, future studies should further investigate this, for example by using physiological measures in combination with experiments (see “Future directions”). Second, it is possible that orang-utan females will especially employ an attraction-filter during ovulation. In Chapter 8, I have described two cases that suggest increased sensitivity for flanged male signals, visual or auditory, during ovulation. This idea is also in line with behavioural evidence from wild Bornean orang-utan females, who selectively mate with flanged males only during their ovulation (Knott et al., 2009). Third, the idea of an attraction-filter does not take into account potential socio-ecological constraints, even though such constraints are essential in shaping female sexual behaviour.

In the case of Bornean orang-utans, populations consist of a relatively large proportion of flanged males, many of which are semi-nomadic (Kunz et al., 2022). Furthermore, the dominance hierarchy between flanged males is often rather unstable (Spillmann et al., 2017). This results in a situation where females can be confronted with a large number of different males, none of which achieves absolute local dominance, and some of which may be infanticidal. Consequently, it may not be adaptive for female Bornean orang-utans to rely purely on an attraction-filter mechanism for mate selection. Instead, females need to strategically spread the probability of paternity across multiple flanged males, to decrease risk of infanticide (Kunz et al., 2022; Palombit, 2015). Still, employing such a sexual counterstrategy against infanticide does not fully rule out an attraction-filter. Because orang-utan females are characterised by concealed ovulation, they might still exert female preference by mating with their most preferred flanged male around ovulation. This would imply that their attraction-filter is activated specifically during their peri-ovulatory period, while outside of this period, females do not discriminate based on attractive traits as much. Importantly, this would allow females to ensure a mate with good genetic quality during their most fertile period, while at the same time reducing infanticide risk by spreading the probability of paternity.

The above-mentioned points are summarised in Figure 2. First, the attraction-filter of Bornean orang-utans encompasses both visual and auditory attractiveness. Second, the sensitivity of this filter is strongly modulated by the ovulatory status of the female (dotted arrow). Third, exertion of female preference can be restricted by socio-ecological factors, such as the need to strategically mate with multiple males to reduce infanticide risk. Altogether, this model suggests that there is still a role for female mate choice despite the need to spread paternity probability, and thus the possibility that sexually selective cognition to some extent guides mate choice by Bornean orang-utan females.

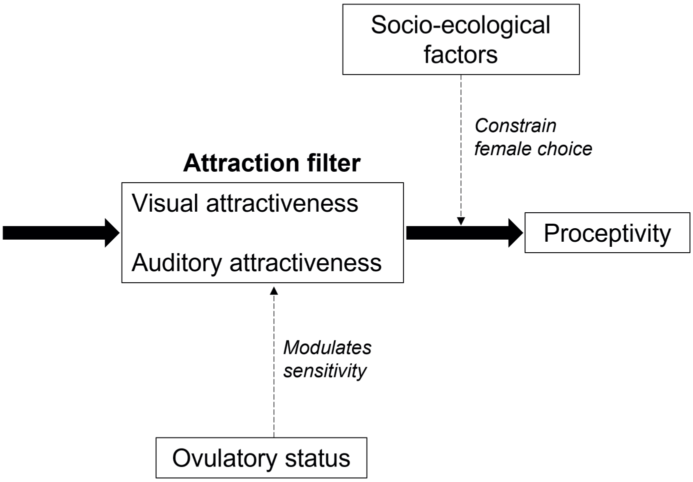


Figure 2. Schematic depiction of the attractiveness filter of female orang-utans, and the two important factors influencing it. First, ovulatory status influences the sensitivity of the filter, so that females are more biased towards specific males during ovulation. However, social-ecological factors, such as the need to reduce infanticide risk, may constrain the link between female preference and actual proceptive behaviour.

Methodological considerations

This thesis encompasses a range of paradigms employed in humans and Bornean orang-utans, each with their own methodological considerations. Since the literature on primates is scarce and new methods are continuously being developed, I therefore focus on the methodological considerations for testing primates, and specifically orang-utans.

Studies of sexually selective cognition in non-human primates remain rare, even though a more systematic approach could help reveal intriguing commonalities and differences between species. In this thesis, I have tried to explore sexually selective cognition in Bornean orang-utans by employing similar test paradigms that have been used to study this topic in humans. However, I was able to employ these paradigms only with mixed success. Based on my experiences, future studies could consider improving their approach in several ways. In the section above, I already argued for a more biocentric approach to animal cognition (Bräuer et al., 2020). Taking such a perspective is essential to ensure that tasks are valid measures of the hypothesized cognitive processes involved in performing the task (Schubiger et al., 2020). I want to elaborate on this in the context of Chapter 6, where I tested Bornean orang-utans in two touchscreen tasks, that both yielded null results.

First, Bornean orang-utans have historically been exposed to extremely long periods of food scarcity (Vogel et al., 2017). As a consequence, orang-utans are extremely well-equipped to saving energy. For example, orang-utans have very low levels of daily energy expenditure compared to other mammals (Pontzer et al., 2010) and will minimise travel costs by adapting their locomotion style (Roth et al., 2017; Thorpe et al., 2007). Whereas sensitivity to food rewards has not been systematically studied yet, it is to be expected that Bornean orang-utans are extremely sensitive to and focused on food rewards. This is also what I noticed in the touchscreen task. At the end of each trial, individuals would receive a reward, in order to keep them motivated. However, it sometimes seemed that the anticipation of a reward distracted them from the task. More specifically, although they performed the task correctly, they showed little involvement in it, and seemed more focused on the reward. Such a finding is not unique to orang-utans, however. In quantity judgment tasks, primates are well-known to show improved performance when they need to discriminate between abstract tokens instead of actual food items (e.g., Boysen & Berntson, 1995). This suggests that primates are naturally inclined to respond to rewarding stimuli, which might disrupt their ability to focus on and complete tasks effectively. Interestingly, I did not encounter the same problem during the eye-tracking experiment (Chapter 7), where individuals received a reward continuously throughout the trial. This design might have avoided continuous anticipation of reward, thereby increasing involvement in the task. Therefore, I consider studies that can provide a reward to orang-utans while they are performing a test trial more likely to be successful.

Second, the touchscreen setup employed in Chapter 6 allowed orang-utans to only use their hands during the tasks. However, manual tasks may not be the most suitable tasks for orang-utans, as they often seem to employ their mouth for manipulating objects or using tools (Bardo et al., 2017). Due to their almost exclusively arboreal life style, orang-utans often need most of their hands and feet to navigate the canopy. Their mouth functions as a ‘fifth’ hand for precise, motoric tasks (Lameira, 2023). Thus, when designing touchscreen tasks for orang-utans, it would be ideal to provide them with the opportunity to use their lips to control the screen. Luckily, systems that allow for this are already available (e.g., Schmitt, 2019), and could be applied more widely in future studies to better accommodate the preferences of participating orang-utans.

Another consideration for future studies refers to the cognitive processes that I have focused on. Whereas Chapter 2 outlines multiple promising methods to study sexually cognition, focusing on attention, memory, and motivational processing, I have mostly focused on attentional processes in this thesis. This is for a large part the result of the COVID-19 pandemic, which has considerably reduced opportunities for research with the orang-utans. While the initial idea was to also study memory for and motivational processing of flanged male stimuli, this became untenable due to the pandemic. However, future projects should ideally employ tasks that measure multiple aspects of sexually selective cognition, so that results can be compared for different aspects of sexually selective cognition. This will also help to elucidate the underlying motives for existing cognitive biases. For example, while an attentional bias can be reflective of both positive or negative interest in a stimulus, this is less likely to be the case in a motivational processing task, where an individual chooses to be exposed to a stimulus. Thus, employing multiple paradigms potentially allows for clearer understanding of the motives that guide cognitive biases.

I find it important to note that one of the methods employed in this thesis, namely the dot-probe paradigm, has come under scrutiny in the psychopathology literature in the last decade. The main issues with the paradigm are its relatively poor reliability (e.g., Kappenman et al., 2014; Rodebaugh et al., 2016), lack of ability to discriminate between different attentional processes (e.g., Belopolsky et al., 2011; Koster et al., 2004), and, consequently, discrepancies in findings. With regard to reliability, previous work has identified low internal (Chapman et al., 2019) and external consistency (Jones et al., 2018), while the discussion about attentional processes mainly revolves around the question whether the dot-probe paradigm measures engagement or disengagement of attention (Belopolsky et al., 2011; Fox et al., 2002; Koster et al., 2004). Interestingly, inconsistent results have also been found in primates with the dot-probe paradigm. While the paradigm has been successful in elucidating the effect of emotion information on cognition in multiple primate species (King et al., 2012; Kret et al., 2016; Lacreuse et al., 2013; Schino et al., 2020; van Berlo et al., 2023), inconsistencies remain as well, as both chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018) and Bornean orang-utans (Laméris et al., 2022) do not seem to show the expected attentional bias towards emotions in the dot-probe task. One important methodological explanation for these inconsistencies is that the dot-probe paradigm relies on reaction times as a measure of attention. However, reaction times are inherently noisy (Morís Fernández & Vadillo, 2020) and may involve trade-offs with accuracy (Draheim et al., 2019). Especially in species with reduced manual dexterity compared to humans, this may obfuscate existing biases. Some of these issues can be resolved by employing non-invasive eye-tracking, as I did in Chapter 7. These methods allow disentangling different attentional processes (Clauss et al., 2022), and, speaking from own experience, seem to yield less noisy data compared to reaction time tasks.

Thus, even though the dot-probe paradigm has helped to gain insight into attentional processes of primates, I consider eye-tracking a better alternative, because it yields more reliable and less noisy data, thereby allowing for a more fine-scaled analysis of different attentional processes. It is important to note that eye-tracking is especially suitable for investigating overt attentional processes, because it relies on eye movements. However, attention also operates *without* eye movements, a process referred to as covert attention. Covert attention refers to a shift in focus, that precedes eye movements (Weierich et al., 2008). Nonetheless, employing eye-tracking in combination with cuing tasks allows one to distinguish between covert and overt attention by investigating whether attentional biases are present in the absence of eye movements (e.g., Petrova et al., 2013), although such study designs might be too complex for non-restraint experiments in primates. Concluding, eye-tracking seems a more suitable method to investigate *overt* attentional processes in primates, but cannot give insight into *covert* attention in primates.

Practical implications

In Chapter 5, I showed that initial attraction during a speed-date predicts fixation duration in an eye-tracking task. This result establishes a link between attentional biases and subsequent behaviour. While previous research has established such a link at trait level (Eastwick et al., 2011), I demonstrated that cognitive tasks might be predictive of differential behaviour towards potential mates instead of a general tendency to evaluate potential mates as suitable or not. In other words, this finding suggests that attraction to another is reflected in implicit cognitive processes. Dating apps or websites could therefore consider a more cognitive-based approach to identifying preferred partners. Currently, dating websites mostly rely on self-reported personality information and attitudes, and explicitly stated preferences. Dating apps like Tinder, on the other hand, rely on sequential presentation of potential partners. Both of these have important shortcomings. First, several studies have shown that explicitly stated preferences for personality traits in potential partners fail to predict initial mate choice (Eastwick & Finkel, 2008; Joel et al., 2017; Tidwell et al., 2013). Second, in sequential presentation paradigms of faces, people tend to develop suboptimal sampling heuristics (Furl et al., 2019; Lee & Courey, 2020).

To solve these issues, dating websites and apps could try to implement a more implicit first filter by using eye-tracking tasks for example. Recent developments in webcam- (Semmelmann & Weigelt, 2018) or even smartphone-based eye-tracking (Valliappan et al., 2020) allow for measuring attentional preferences by presenting a grid of pictures of potential partners. These attentional preferences could be considered the first filter, after which people can further explore the profiles of the potential partners that they attended to. The benefit of such an approach is that it fits more closely with the human mate choice process: it allows participants to implicitly sample different options based on visual cues, without inducing decision-making biases that are characteristic of dating apps like Tinder. After applying such a first filter, users could be allowed to further explore the profiles and pictures of potential mates that attracted their attention, so that there is still room for exercising explicit preferences.

Another practical goal of this thesis was to explore methods to identify mate preferences of zoo-housed orang-utans. Reproductive success of zoo-housed orang-utans is relatively low compared to other great ape species (Kaumanns et al., 2004). Developing methods to identify individual mate preferences could potentially help to solve this, as it would allow for better matching of individuals across zoos (Asa et al., 2011). However, based on the results presented in this thesis, such methods do not yet seem feasible for application within the orang-utan breeding programme. Apart from the methodological considerations (see section above), there are some other caveats that should be addressed before such an approach can be considered useful.

First, while I found a robust bias towards flanged male stimuli in the eye-tracking experiments described in Chapter 7, I did not find clear indications of subtle individual attentional preferences in Experiment 2, where individuals were presented with multiple stimuli of four different males. While I found a few robust biases towards one specific flanged male compared to the unflanged males, none of the females seemed to attend more to one specific flanged male compared to another flanged male. This is not to say that it would be impossible to identify such preferences via eye-tracking. However, it would require larger samples than studies that investigate attentional biases towards a specific stimulus category. This may not be feasible in zoos, because it would be a time-consuming endeavour. Instead, it might be more promising to develop methods that require little time investment and are intrinsically rewarding for participants. For example, one could explore designs in which individuals self-expose to stimuli or can trigger video calls with or video fragments of different conspecifics. For example, a recent study in parrots (order *Psittaciformes*) employed a free-choice paradigm where individuals could trigger video calls with other parrots and interact with them (Kleinberger et al., 2023). Given that such methods rely on intrinsic motivation, they may be better suited to investigate individual preferences compared to extrinsically rewarded tasks.

Second, it will be important to establish a link between performance or biases in cognitive tasks and later behaviour. For example, if we assume that we can reliably measure a cognitive preference towards one specific individual over another, would this also translate into more affiliation or even a higher probability of successful reproduction with this individual? This thesis suggests that such a link may exist in humans, at least when considering the eye-tracking results. However, a similar link has, to my knowledge, not yet been established in non-human primates.

A final practical implication from this thesis concerns the ovulatory shift in female preferences. In Chapter 8, I reported two cases of Bornean orang-utan females who were especially sensitive to flanged male signals (auditory or visual) in their peri-ovulatory period. This corroborates findings from wild Bornean orang-utans (Knott et al., 2009), and may also be relevant for the future development of test paradigms to identify mate preferences. As I argued in the “Theoretical implications”-section, it could be the case that the attraction-filter is especially sensitive during ovulation. Unfortunately, I could not control for ovulation status during the cognitive tasks. Female primates in zoos and sanctuaries are often on birth control or have a dependent infant, which makes it difficult to control for ovulation status during experiments. However, the results of Chapter 8 suggest that investigating cognitive biases towards potential mates would ideally be performed when a female is ovulating. At this point, her biases are most likely to reflect mating motivation, thereby probably making them a more reliable predictor of actual mate choice.

Future directions

Based on the implications and considerations outlined above, I will now suggest some future directions for research on mate choice and sexually selective cognition.

First, research on cognition and mate choice would benefit from more ecologically valid paradigms to establish links between ratings of attractiveness, cognitive biases, and proxies of mate choice. Chapter 3 and 5 of this thesis provide examples of such an approach in humans, employing speed-dating as a proxy of mate choice (Finkel & Eastwick, 2008). In general, researchers have typically examined the role of attractiveness in human mate choice through isolated experiments where participants rated various samples in terms of attractiveness. Subsequently, these ratings are frequently associated with sample characteristics that are thought to reflect mate quality, such as masculinity and femininity (e.g., Collins & Missing, 2003; Little, Connely, et al., 2011). I see two main issues with this approach, the first of which concerns the fact that this approach lacks ecological validity due to the isolated setting in which the stimuli are presented. For example, subtle differences in isolated olfactory cues might indeed be correlated with attractiveness ratings. However, this does not mean that in a natural setting these subtle differences can be perceived at all, let alone have an effect on human mate choice. Secondly, the traditional approach does not help to establish a link between cues and mate choice behaviour. This link is often implicitly assumed to be there when certain cues are considered attractive. Thus, finding a link between cues that play a role in mate choice and actual mate choice should be a priority in future work.

This last point also applies to future work on animal cognition in general. While researchers often investigate cognitive biases using computerized experiments in animals, they are hardly ever linked to behaviour. One exception in non-human primates comes to mind. Ryan et al. (2020) performed an eye-tracking task with infant rhesus macaques, where they measured how long each individual fixated on eyes in facial stimuli. They correlated this to actual social behaviour, and found that individuals that spent more time fixating on eyes during the eye-tracking task were also more likely to initiate social interactions. Even though this study shows a trait-level association between looking behaviour and actual social behaviour, and not a link between attentional preferences to social preferences per se, similar studies could help to gain a better understanding of the link between social cognition and social behaviour. While such studies have not yet been performed with regard to mate choice in non-human primates, there are examples from other species. For example, in zebra finches (*Taeniopygia guttata*), female preferences in an operant and playback experiment that exposes females to male calls corresponds with female preferences in a live mate choice context (Holveck & Riebel, 2007). Other work has shown that allowing females to exert their preferences is associated with higher reproductive success (Ihle et al., 2015). More work on this topic in non-human primates is essential to understand whether preference tasks can be used to predict mate preferences.

Furthermore, future studies could consider a more physiological approach to studying mate choice. Measurement of physiological information has already been used to study initial attraction in speed-date studies (Prochazkova et al., 2022; Zeevi et al., 2022). However, these measures could also be combined with cognitive tasks. In the context of mate choice, this has recently been done by Pronk et al. (2021), who presented participants with multiple dating profiles and measured pupil diameter while participants were scanning these profiles. Participants who showed pupil dilation while scanning a profile, were more likely to select this profile as a suitable partner. Similarly, evidence indicates that heart rate variability concords with sexual arousal (Lorenz et al., 2012). Another physiological measure, facial temperature, has recently been shown to vary as a function of emotional valence in humans (Aristizabal-Tique et al., 2023), although some studies argue that facial temperature provides only information about arousal (Kosonogov et al., 2017). Conveniently, most of these physiological measures can also be assessed to some extent in non-human primates non-invasively (pupil: Kret et al., 2014; facial temperature: Kuraoka & Nakamura, 2022;

heart rate: Unakafov et al., 2018; Wang et al., 2023), although heart rate variability cannot yet be estimated non-invasively (Madan et al., 2018). Thus, combining these measures with cognitive tasks can potentially help to determine whether cognitive biases are the result of positive or negative valence. In the end, this is an essential step for establishing a link between motivational state and cognitive biases.

One further line of research that deserves attention in future research is measurement of individual preferences in primates. Currently employed cognitive tasks, including the ones described in this thesis, mostly rely on categorical designs, aiming to identify a preference or bias for one category over another *across individuals.* However, when considering mate choice, it is well-known that individuals can vary in their mate preferences (Jennions & Petrie, 1997). To capture such inter-individual variation in preferences, it will be necessary to develop suitable test designs. One example comes from systematic investigations of individual food preference in primates (Hopper et al., 2019; Huskisson et al., 2020, 2021). This line of research has shown that simple computerised paired presentation tasks can be used to identify individual preferences for food, and that these preferences are consistent across tasks. I suggest future studies should employ this approach beyond food preferences to gain a better insight into individual preferences for specific stimuli or, in the case of sexually selective cognition, specific potential mates.

Conclusion

Recent psychological research has suggested an important role for cognitive processes in human mate choice. In this dissertation, I have taken a closer look at these processes in humans, and investigated whether these are also present in Bornean orang-utans by running a set of comparative studies. The thesis has shown that attractiveness-based attentional biases are clearly present in humans, and that such biases might also be related to actual mate choice. When it comes to Bornean orang-utans, the findings are mixed: they did not show any biases in touchscreen tasks, but did have an attentional bias towards flanged males across two eye-tracking experiments. Furthermore, auditory signals may play a more important role in orang-utan compared to human mate choice. Even though the results of this thesis suggest that both humans and orang-utans have an attraction-filter that is reflected in cognitive biases towards mate-relevant traits, a better understanding of the link between such biases and actual mate choice remains of pivotal importance. Furthermore, future studies should employ test paradigms that tap into different cognitive processes, and consider incorporating non-invasive measures of physiology. This could help to elucidate the valence underlying cognitive biases that might be functional in a mate choice context. Finally, although current paradigms might not yet be suitable for testing attraction on an individual basis, future studies can use the findings and recommendations from this thesis to work toward the goal of identifying individual mate preferences.

Appendices

Appendix A: Supplementary Material for Chapter 2

Supplementary Table 1 – Overview of studies on sexually selective cognition in primates.

Study	Method	Species	Main finding
Waitt et al., 2003	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Females showed an attentional bias towards red male faces compared to more pale faces.
Cooper & Hosey, 2003	Preferential looking (sequential)	Common brown lemur (*Eulemur vulvus*) & controls that do not experience sexual dichromatism (*Lemuridae)*	Common brown lemur females showed an attentional bias towards more brightly coloured male pelage, while this was not the case for the control individuals, suggesting that sexual dichromatism plays a role in mate choice.
Deaner et al., 2005	Preference task	Rhesus macaque (*Macaca mulatta*)	Male macaques could choose to see an empty screen or a picture, with each choice receiving different kinds of rewards. Results showed that macaques were willing to give up reward to see pictures of high-status faces and perinea.
Waitt & Little, 2006	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Macaques showed an attentional bias towards symmetrized faces. However, this effect was especially driven by female observers.
Waitt et al., 2006	Preferential looking (sequential)	Rhesus macaque (*Macaca mulatta*)	Males show more attention to pictures of reddened female hindquarters compared to less red hindquarters. This effect was not found for female faces.
Gerald et al., 2007	Preferential looking (sequential)	Rhesus macaque (*Macaca mulatta*)	Females show more attention to pictures of reddened female faces and hindquarters compared with more pale versions of the same picture.
Lacreuse et al., 2007	Effort	Rhesus macaque (*Macaca mulatta*)	Ovulating females, but not non-ovulating female, pressed longer when they would see a male face than a female face. However, they only showed this effect for same-species stimuli.
Higham et al., 2011	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Males looked longer at faces of ovulating females when paired with faces of non-ovulating females. This effect was especially pronounced when males were shown pictures of familiar females.
Watson et al., 2012	Preference test	Rhesus macaque (*Macaca mulatta*)	In a preference task, female macaques could choose to either see a picture or an empty screen. They picked the picture-option most frequently when they knew the picture would be of either a perineum or of a high-status face.
Pflüger et al., 2014	Preferential looking (simultaneous)	Japanese macaque (*Macaca fuscata*)	Males looked longer at faces of intensely coloured female faces.

Supplementary Table 1 – continued

Study	Method	Species	Main finding
Dubuc et al., 2016	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Both males and females look longer at dark red male faces. However, when considering the proportion of subjects that looked longer at dark red faces regardless of preference strength, only females showed a significant dark red bias.
Paukner et al., 2017	Preferential looking (simultaneous)	Capuchin monkey (*Sapajus apella*)	Males showed an attentional bias for symmetrical male faces when paired with asymmetrical male faces, but not symmetrical female faces that were paired with asymmetrical female faces. Females, on the other hand, did not show an attentional bias in either condition.
Damon et al., 2017	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	3-month-old macaques show an attentional bias towards “average” macaque faces, similar to human infants.
Tomeo et al., 2017	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Macaques showed an attentional bias towards individuals faces instead of composite faces, suggesting that they do not prefer averageness.
Lonsdorf et al., 2018	Preferential looking (simultaneous)	Capuchin monkey (*Sapajus apella*)	Females showed a same-sex attentional bias, while males showed no significant bias.
Acikalin et al., 2018	Preference test	Rhesus macaque (*Macaca mulatta*)	Macaques preferred brand logos that they associated with pictures of high-status faces or perinea.
Damon et al., 2019	Preferential looking (sequential)	Rhesus macaque (*Macaca mulatta*)	Macaques show a species-specific bias for attractive faces, just like humans.
Rosenfield et al., 2019	Preferential looking (simultaneous)	Rhesus macaque (*Macaca mulatta*)	Female macaques show an attentional bias towards masculine male faces that were paired with more feminine male faces. However, this was only the case when the difference in masculinity between the faces was most pronounced.

Appendix B: Supplementary Material for Chapter 3

Supplementary Table 1 - Model table for the logistic regressions predicting propensity to date again from post-date attractiveness and long-term partner suitability ratings.

	Propensity to date again			
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Intercept	0.21	0.12 – 0.34	0.39	0.23 – 0.64
rater sex [M]	1.31	0.74 – 2.35	1.47	0.82 – 2.60
post-date attractiveness	5.68	4.00 – 8.41		
rater sex [M]:post-date attractiveness	1.88	1.18 – 3.04		
post-date long-term rating			5.59	3.98 – 8.16
rater sex [M]:post-date long-term rating			1.69	1.07 – 2.71
Random effects	Estimate	CI (89%)	Estimate	CI (89%)
sd [Intercept] participant	1.10	0.65 – 1.58	1.41	0.94 – 1.94
sd [post-date attractiveness] participant	0.38	0.05 – 0.77		
sd [post-date long-term rating] participant			0.38	0.06 – 0.76
sd [Intercept] partner	1.08	0.62 – 1.57	0.95	0.39 – 1.50
N	67 $_{\text{pp}}$		67 $_{\text{pp}}$	
	67 $_{\text{partner}}$		67 $_{\text{partner}}$	
Observations	554		554	

Supplementary Table 2 – Effect sizes for the logistic regressions predicting propensity to date again from post-date attractiveness and long-term partner suitability ratings.’

Predictor	*Rater sex*	*Median OR*	*CrI 89%*	*pd*	*d*	*N*
attractiveness	female	5.68 [1.30]	4.00; 8.41	1.00	0.96 [0.13]	554
attractiveness	male	10.61 [3.06]	6.92; 17.92	1.00	1.30 [0.16]	
long-term	female	5.59 [1.24]	3.98; 8.16	1.00	0.95 [0.12]	
long-term	male	9.37 [2.61]	6.14; 15.53	1.00	1.23 [0.16]	

Supplementary Table 3 – Model table for the ordinal regressions between visual attractiveness rating and long-term rating. Dependent variables are in bold

	Visual attractiveness rating		**Visual long-term rating**	
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.00	0.00 – 0.00	0.00	0.00 – 0.00
Threshold.2.	0.03	0.01 – 0.04	0.07	0.04 – 0.13
Threshold.3.	0.25	0.15 – 0.40	0.70	0.42 – 1.18
Threshold.4.	3.69	2.25 – 6.16	9.33	5.36 – 16.67
Threshold.5.	47.45	26.09 – 89.41	105.74	53.54 – 221.66
Threshold.6.	1108.79	436.90 – 3190.56	4769.71	1535.19 – 16746.93
long-term rating	8.14	6.33 – 10.61		
rater sex [M]	1.16	0.70 – 1.96	1.19	0.68 – 2.04
long-term rating:rater sex [M]	0.97	0.75 – 1.26		
attractiveness rating			7.11	5.27 – 9.68
attractiveness rating:rater sex [M]			1.97	1.39 – 2.83
Random effects	Estimate	CI (89%)	Estimate	CI (89%)
sd [Intercept] participant	1.03	0.74 – 1.35	1.46	1.15 – 1.80
sd [attractiveness rating] participant			0.72	0.51 – 0.96
sd [long-term rating] participant	0.29	0.08 – 0.49		
sd [Intercept] partner	0.79	0.53 – 1.06	0.46	0.13 – 0.75
N	$58_{\text{participant}}$		$58_{\text{participant}}$	
	59_{partner}		59_{partner}	
Observations	482		482	

Supplementary Table 4 – Model table for the ordinal regressions between auditory attractiveness rating and long-term rating. Dependent variables are in bold.

Predictors	**Auditory attractiveness rating**		**Auditory long-term rating**	
	Odds Ratios	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.00	0.00 – 0.00	0.00	0.00 – 0.00
Threshold.2.	0.00	0.00 – 0.01	0.04	0.02 – 0.07
Threshold.3.	0.12	0.07 – 0.18	0.48	0.29 – 0.79
Threshold.4.	1.93	1.24 – 3.00	10.15	6.07 – 17.42
Threshold.5.	42.24	24.84 – 75.27	162.56	88.26 – 316.36
Threshold.6.	1291.53	598.32 – 3142.25	7094.86	2793.92 – 19513.68
long-term rating	11.82	9.08 – 15.63		
rater sex [M]	0.92	0.58 – 1.47	1.24	0.73 – 2.08
long-term rating:rater sex [M]	1.07	0.84 – 1.41		
attractiveness rating			12.20	9.47 – 15.87
attractiveness rating:rater sex [M]			1.38	1.08 – 1.81
Random effects	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*
sd [Intercept] participant	0.98	0.72 – 1.26	1.42	1.12 – 1.75
sd [attractiveness rating] participant			0.22	0.03 – 0.46
sd [long-term rating] participant	0.28	0.05 – 0.49		
sd [Intercept] partner	0.57	0.27 – 0.84	0.22	0.02 – 0.49
N	59 $_{\text{participant}}$ 58 $_{\text{partner}}$		59 $_{\text{participant}}$ 58 $_{\text{partner}}$	
Observations	481		481	

Supplementary Table 5 – Model table for the ordinal regressions between olfactory attractiveness rating and long-term rating. Dependent variables are in bold.

	Olfactory attractiveness rating		**Olfactory long-term rating**	
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.00	0.00 – 0.00	0.00	0.00 – 0.00
Threshold.2.	0.02	0.02 – 0.04	0.04	0.02 – 0.06
Threshold.3.	0.26	0.18 – 0.39	0.36	0.23 – 0.55
Threshold.4.	2.60	1.79 – 3.76	4.93	3.20 – 7.70
Threshold.5.	31.57	20.24 – 50.33	96.52	55.14 – 175.00
Threshold.6.	534.49	288.02 – 1027.61	5005.33	2012.81 – 13620.72
long-term rating	9.96	8.02 – 12.52		
rater sex [M]	1.20	0.79 – 1.81	1.11	0.70 – 1.78
long-term rating:rater sex [M]	0.90	0.72 – 1.12		
attractiveness rating			10.20	7.86 – 13.41
attractiveness rating:rater sex [M]			1.21	0.88 – 1.69
Random effects	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*
sd [Intercept] participant	0.93	0.71 – 0.18	1.22	0.96 – 1.52
sd [attractiveness rating] participant			0.71	0.54 – 0.90
sd [long-term rating] participant	0.26	0.08 – 0.44		
sd [Intercept] partner	0.27	0.04 – 0.54	0.23	0.02 – 0.49
N	$66_{\text{participant}}$ 67_{partner}		$66_{\text{participant}}$ 67_{partner}	
Observations	523		523	

Supplementary Table 6 – Effect sizes for the ordinal regressions between attractiveness rating and long-term rating per modality.

Modality	*Dependent*	*Predictor*	*Rater sex*	*Median OR*	*CrI 89%*	*pd*	*d*	*N*
visual	attractiveness	long-term	female	8.14 [1.30]	6.33; 10.61	1	1.16 [0.09]	482
visual	attractiveness	long-term	male	7.86 [1.18]	6.23; 10.11	1	1.14 [0.08]	
visual	long-term	attractiveness	female	7.11 [1.31]	5.27; 9.68	1	1.08 [0.10]	
visual	long-term	attractiveness	male	14.04 [2.85]	10.22; 19.60	1	1.46 [0.11]	
auditory	attractiveness	long-term	female	11.82 [1.99]	9.08; 15.63	1	1.36 [0.09]	481
auditory	attractiveness	long-term	male	12.75 [2.08]	9.88; 16.89	1	1.40 [0.09]	
auditory	long-term	attractiveness	female	12.20 [1.94]	9.47; 15.87	1	1.38 [0.09]	
auditory	long-term	attractiveness	male	16.95 [2.99]	12.89; 22.66	1	1.56 [0.10]	
olfactory	attractiveness	long-term	female	9.96 [1.38]	8.02; 12.52	1	1.27 [0.08]	523
olfactory	attractiveness	long-term	male	8.93 [1.30]	7.15; 11.47	1	1.21 [0.08]	
olfactory	long-term	attractiveness	female	10.2 [1.70]	7.86; 13.41	1	1.28 [0.09]	
olfactory	long-term	attractiveness	male	12.36 [2.40]	9.12; 17.03	1	1.39 [0.11]	

Supplementary Table 7 – Model table for the independent logistic regressions, separately testing the effect of attractiveness in each modality on propensity to date again.

	Propensity to date again					
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Intercept	0.63	0.39 – 1.04	0.39	0.22 – 0.69	0.27	0.16 – 0.46
rater sex [M]	1.63	0.92 – 2.81	1.44	0.77 – 2.64	1.81	0.99 – 3.27
visual attractiveness	2.01	1.59 – 2.61				
rater sex [M]:visual attractiveness	1.45	1.04 – 2.05				
auditory attractiveness			1.26	0.98 – 1.65		
rater sex [M]:auditory attractiveness			1.03	0.74 – 1.44		
olfactory attractiveness					0.82	0.66 – 0.99
rater sex [M]:olfactory attractiveness					1.33	1.01 – 1.76
Random effects	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*
sd [Intercept] participant	0.98	0.60 – 1.40	1.24	0.85 – 1.68	1.28	0.92 – 1.69
sd [attractiveness rating] participant	0.23	0.02 – 0.53	0.36	0.07 – 0.65	0.14	0.01 – 0.34
sd [Intercept] partner	1.10	0.74 – 1.51	1.55	1.14 – 2.02	1.51	1.14 – 1.95
N	$58_{\text{participant}}$ 59_{partner}		$59_{\text{participant}}$ 58_{partner}		$67_{\text{participant}}$ 67_{partner}	
Observations	482		481		533	

Supplementary Table 8 - Model table for the ordinal regressions between auditory and visual attractiveness ratings. Dependent variables are in bold.

	Auditory attractiveness		**Visual attractiveness**	
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.01	0.01 – 0.03	0.03	0.02 – 0.06
Threshold.2.	0.10	0.06 – 0.16	0.38	0.21 – 0.66
Threshold.3.	0.44	0.27 – 0.71	1.47	0.84 – 2.58
Threshold.4.	1.62	1.01 – 2.62	7.58	4.24 – 13.63
Threshold.5.	7.15	4.40 – 11.87	40.18	21.27 – 77.12
Threshold.6.	53.99	29.92 – 100.41	360.35	158.86 – 896.16
visual attractiveness	1.30	1.09 – 1.56		
rater sex [M]	1.30	0.77 – 2.21	1.29	0.71 – 2.31
visual attractiveness:rater sex [M]	1.06	0.83 – 1.36		
auditory attractiveness			1.25	1.04 – 1.52
auditory attractiveness:rater sex [M]			1.02	0.80 – 1.29
Random effects	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*
sd [Intercept] participant	1.16	0.84 – 1.54	0.70	0.35 – 1.07
sd [visual attractiveness] participant			0.17	0.01 – 0.39
sd [auditory attractiveness] participant	0.10	0.00 – 0.28		
sd [Intercept] partner	1.60	1.25 – 2.03	1.25	0.94 – 1.63
N	$58_{\text{participant}}$ 58_{partner}		$58_{\text{participant}}$ 58_{partner}	
Observations	473		473	

Supplementary Table 9 - Model table for the ordinal regressions between olfactory and visual attractiveness ratings. Dependent variables are in bold.

	Olfactory attractiveness		**Visual attractiveness**	
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.04	0.02 – 0.06	0.04	0.02 – 0.07
Threshold.2.	0.19	0.12 – 0.32	0.38	0.21 – 0.65
Threshold.3.	0.65	0.40 – 1.06	1.42	0.81 – 2.47
Threshold.4.	1.97	1.21 – 3.19	6.66	3.77 – 11.87
Threshold.5.	8.52	5.16 – 14.27	36.02	19.30 – 68.75
Threshold.6.	49.60	27.83 – 92.77	332.24	145.70 – 823.36
visual attractiveness	1.24	1.04 – 1.47		
rater sex [M]	1.52	0.89 – 2.59	1.25	0.69 – 2.23
visual attractiveness:rater sex [M]	0.99	0.79 – 1.26		
olfactory attractiveness			1.21	1.03 – 1.42
olfactory attractiveness:rater sex [M]			0.99	0.79 – 1.23
Random effects	**Estimate**	**CI (89%)**	**Estimate**	**CI (89%)**
sd [Intercept] participant	0.93	0.63 – 1.29	1.15	0.84 – 1.51
sd [visual attractiveness] participant	0.12	0.00 – 0.32		
sd [olfactory attractiveness] participant			0.10	0.00 – 0.29
sd [Intercept] partner	1.18	0.87 – 1.54	1.56	1.22 – 1.98
N	$58_{\text{participant}}$ 59_{partner}		$58_{\text{participant}}$ 59_{partner}	
Observations	465		465	

Supplementary Table 10 - Model table for the ordinal regressions between olfactory and auditory attractiveness ratings. Dependent variables are in bold.

	Olfactory attractiveness		**Auditory attractiveness**	
Predictors	*Odds Ratios*	*CI (89%)*	*Odds Ratios*	*CI (89%)*
Threshold.1.	0.04	0.02 – 0.07	0.02	0.01 – 0.03
Threshold.2.	0.23	0.14 – 0.36	0.12	0.07 – 0.19
Threshold.3.	0.76	0.48 – 1.19	0.53	0.34 – 0.83
Threshold.4.	2.18	1.37 – 3.46	1.92	1.23 – 3.02
Threshold.5.	8.99	5.57 – 14.69	8.46	5.30 – 13.72
Threshold.6.	52.94	29.91 – 95.91	60.81	33.64 – 112.95
auditory attractiveness	1.20	1.00 – 1.44		
rater sex [M]	1.56	0.93 – 2.58	1.27	0.77 – 2.11
auditory attractiveness:rater sex [M]	0.93	0.74 – 1.18		
olfactory attractiveness			1.15	0.98 – 1.34
olfactory attractiveness:rater sex [M]			0.98	0.79 – 1.21
Random effects	*Estimate*	*CI (89%)*	*Estimate*	*CI (89%)*
sd [Intercept] participant	0.92	0.67 – 1.18	0.76	0.52 – 1.02
sd [olfactory attractiveness] participant			0.10	0.01 – 0.25
sd [auditory attractiveness] participant	0.11	0.01 – 0.27		
sd [Intercept] partner	1.10	0.86 – 1.37	1.17	0.92 – 1.45
N	$59_{\text{participant}}$ 58_{partner}		$59_{\text{participant}}$ 58_{partner}	
Observations	465		465	

Supplementary Table 11 – Model table for the partial logistic regression model, testing the effect of attractiveness in each modality on propensity to date again.

	Propensity to date again	
Predictors	*Odds Ratios*	*CI (89%)*
Intercept	0.59	0.35 – 1.00
rater sex [M]	1.62	0.90 – 2.89
visual attractiveness	2.25	1.71 – 3.06
olfactory attractiveness	0.73	0.57 – 0.92
auditory attractiveness	1.17	0.89 – 1.55
rater sex [M]:visual attractiveness	1.38	0.96 – 2.03
rater sex [M]:olfactory attractiveness	1.27	0.93 – 1.75
rater sex [M]:auditory attractiveness	1.12	0.78 – 1.61
Random effects	*Estimate*	*CI (89%)*
sd [Intercept] participant	1.12	0.50 – 1.79
sd [visual attractiveness] participant	0.30	0.01 – 0.77
sd [auditory attractiveness] participant	0.41	0.03 – 0.87
sd [olfactory attractiveness] participant	0.21	0.01 – 0.56
sd [Intercept] partner	1.12	0.58 – 1.76
N	$58_{\text{participant}}$ 58_{partner}	
Observations	457	

Appendix C: Supplementary Material for Chapter 5

Supplementary Table 1 - Model table for the Bayesian mixed model that predicts RT from Pre-date attractiveness rating and Gender.

	RT	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.52	-1.18 – 2.22
Gender[Female]	0.34	-1.37 – 2.05
AttractivenessDistractor	1.44	0.18 – 2.69
AttractivenessProbe	-1.09	-2.51 – 0.29
Gender[Female]: AttractivenessDistractor	-0.41	-1.68 – 0.86
Gender[Female]: AttractivenessProbe	1.40	-0.02 – 2.82
Random Effects		
σ^2	2588.90	
$\tau_{00\ \text{Subject}}$	0.97	
$\tau_{11\ \text{Subject:AttractivenessDistractor}}$	7.60	
$\tau_{11\ \text{Subject:AttractivenessProbe}}$	13.47	
N_{Subject}	57	
Observations	4831	

Notes: Gender was sum-coded, while Pre-date attractiveness ratings were centered around 4 (the middle option).

Supplementary Table 2 - Model table for the Bayesian mixed model that predicts RT from Post-date attractiveness ratings and Gender.

	RT	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.36	-1.42 – 2.14
Gender[Female]	-0.24	-2.06 – 1.64
AttractivenessDistractor	1.89	0.66 – 3.11
AttractivenessProbe	-0.89	-2.44 – 0.63
Gender[Female]: AttractivenessDistractor	0.34	-0.89 – 1.59
Gender[Female]: AttractivenessProbe	1.16	-0.41 – 2.71
Random Effects		
σ^2	2580.38	
$\tau_{00\ \text{Subject}}$	1.29	
$\tau_{11\ \text{Subject:AttractivenessDistractor}}$	1.92	
$\tau_{11\ \text{Subject:AttractivenessProbe}}$	13.50	
N_{Subject}	56	
Observations	3251	

Notes: Gender was sum-coded, while Post-date attractiveness ratings were centered around 4 (the middle option).

Table S3 - Model table for the Bayesian mixed model that predicts RT from Date outcome and Gender.

	RT	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.82	-1.14 – 2.82
Gender[Female]	0.97	-1.08 – 2.99
DateAgainProbe[yes]	-0.81	-3.16 – 1.45
DateAgainDistractor[yes]	2.20	0.22 – 4.24
Gender[Female]:DateAgainProbe[yes]	2.31	0.00 – 4.66
Gender[Female]:DateAgainDistractor[yes]	0.62	-1.42 – 2.67
Random Effects		
σ^2	2588.97	
$\tau_{00\ \text{Subject}}$	1.60	
$\tau_{11\ \text{Subject:DateAgainProbe[yes]}}$	26.92	
$\tau_{11\ \text{Subject:DateAgainDistractor[yes]}}$	4.71	
N_{Subject}	56	
Observations	3251	

Notes: All predictors were sum-coded.

Supplementary Table 4 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Pre-date attractiveness rating and Gender.

	Left bias	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.97	0.91 – 1.04
phi_Intercept	5.44	4.52 – 6.56
zoi_Intercept	0.02	0.01 – 0.06
coi_Intercept	0.86	0.43 – 1.69
AttractivenessLeft	1.39	1.34 – 1.44
Gender[Female]	1.00	0.94 – 1.06
AttractivenessRight	0.69	0.67 – 0.71
AttractivenessLeft:Gender[Female]	0.98	0.95 – 1.02
Gender[Female]:AttractivenessRight	1.01	0.98 – 1.05
phi_AttractivenessLeft	0.96	0.90 – 1.02
phi_Gender[Female]	0.97	0.80 – 1.17
phi_AttractivenessRight	0.97	0.91 – 1.03
phi_AttractivenessLeft:Gender[Female]	1.02	0.95 – 1.09
phi_Gender[Female]:AttractivenessRight	1.02	0.96 – 1.09
zoi_AttractivenessLeft	1.19	1.00 – 1.43
zoi_Gender[Female]	1.10	0.55 – 2.21
zoi_AttractivenessRight	1.58	1.32 – 1.92
zoi_AttractivenessLeft:Gender[Female]	0.98	0.83 – 1.17
zoi_Gender[Female]:AttractivenessRight	0.93	0.77 – 1.12
coi_AttractivenessLeft	1.93	1.43 – 2.67
coi_Gender[Female]	0.85	0.48 – 1.52
coi_ AttractivenessRight	0.42	0.28 – 0.61
coi_AttractivenessLeft:Gender[Female]	0.86	0.63 – 1.17
coi_Gender[Female]:AttractivenessRight	1.40	0.96 – 2.12
Random Effects		
σ^2	0.01	
$\tau_{00\ \text{Subject}}$	0.06	
N_{Subject}	35	
Observations	1569	

Notes: Gender was sum-coded, while Pre-date attractiveness ratings were centered around 4 (the middle option). Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Supplementary Table 5 – Slope estimates at different levels of Pre-date attractiveness rating (both left and right picture).

Pre-date attractiveness rating left picture	Median estimate [MAD]	89% CrI	Probability of direction
-3	0.068 [.0028]	0.063, 0.072	1.00
-2	0.077 [.0039]	0.071, 0.083	1.00
-1	0.084 [.0048]	0.077, 0.092	1.00
0	0.087 [.0050]	0.079, 0.095	1.00
1	0.083 [.0044]	0.076, 0.090	1.00
2	0.074 [.0032]	0.069, 0.079	1.00
3	0.063 [.0020]	0.059, 0.066	1.00
Pre-date attractiveness rating right picture	**Median estimate [MAD]**	**89% CrI**	**Probability of direction**
-3	-0.078 [.0025]	-0.081, -0.073	1.00
-2	-0.088 [.0038]	-0.094, -0.082	1.00
-1	-0.096 [.0046]	-0.103, -0.088	1.00
0	-0.098 [.0048]	-0.106, -0.091	1.00
1	-0.091 [.0041]	-0.098, -0.085	1.00
2	-0.077 [.0028]	-0.082, -0.073	1.00
3	-0.061 [.0019]	-0.064, -0.058	1.00

Table S6 – Difference in slope between women and men at different levels of Pre-date attractiveness rating (both left and right picture).

Pre-date attractiveness rating left picture	Median estimate [MAD]	89% CrI	Probability of direction
-3	-.0052 [.0055]	-0.014, 0.004	0.83
-2	-.0075 [.0076]	-0.021, 0.004	0.84
-1	-.0094 [.0094]	-0.025, 0.006	0.84
0	-.0097 [.0100]	-0.026, 0.007	0.83
1	-.0075 [.0088]	-0.021, 0.007	0.81
2	-.0043 [.0064]	-0.015, 0.006	0.75
3	-.0013 [.0040]	-0.008, 0.005	0.64
Pre-date attractiveness rating right picture	**Median estimate [MAD]**	**89% CrI**	**Probability of direction**
-3	.000 [.005]	-0.009, 0.010	0.50
-2	.001 [.008]	-0.014, 0.015	0.54
-1	.005 [.009]	-0.014, 0.022	0.70
0	.012 [.010]	-0.006, 0.032	0.91
1	.013 [.008]	-0.002, 0.030	0.95
2	.008 [.006]	-0.003, 0.020	0.94
3	.003 [.004]	-0.004, 0.011	0.82

Supplementary Table 7 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Post-date attractiveness rating and Gender.

	Left bias	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.93	0.85 – 1.01
phi_Intercept	4.49	3.62 – 5.53
zoi_Intercept	0.01	0.00 – 0.04
coi_Intercept	0.70	0.18 – 2.21
AttractivenessLeft	1.21	1.15 – 1.26
Gender[Female]	1.01	0.93 – 1.09
AttractivenessRight	0.79	0.75 – 0.82
AttractivenessLeft:Gender[Female]	0.98	0.94 – 1.02
Gender[Female]:AttractivenessRight	1.07	1.02 – 1.11
phi_AttractivenessLeft	0.90	0.84 – 0.97
phi_Gender[Female]	0.94	0.76 – 1.16
phi_AttractivenessRight	1.02	0.95 – 1.10
phi_AttractivenessLeft:Gender[Female]	1.03	0.95 – 1.10
phi_Gender[Female]:AttractivenessRight	1.00	0.93 – 1.07
zoi_AttractivenessLeft	1.26	0.99 – 1.63
zoi_Gender[Female]	1.09	0.51 – 2.31
zoi_AttractivenessRight	1.60	1.26 – 2.08
zoi_AttractivenessLeft:Gender[Female]	1.07	0.84 – 1.36
zoi_Gender[Female]:AttractivenessRight	0.79	0.61 – 1.00
coi_AttractivenessLeft	1.84	1.19 – 2.95
coi_Gender[Female]	0.98	0.46 – 2.23
coi_ AttractivenessRight	0.57	0.36 – 0.87
coi_AttractivenessLeft:Gender[Female]	0.88	0.56 – 1.45
coi_Gender[Female]:AttractivenessRight	1.14	0.73 – 1.80
Random Effects		
σ^2	0.01	
$\tau_{00\ \mathrm{Subject}}$	0.06	
N_{Subject}	35	
Observations	1009	

Notes: Gender was sum-coded, while Post-date attractiveness ratings were centered around 4 (the middle option). Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Supplementary Table 8 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Date outcome and Gender.

	Left bias	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.87	0.80 – 0.96
phi_Intercept	4.18	3.38 – 5.21
zoi_Intercept	0.02	0.00 – 0.05
coi_Intercept	0.58	0.19 – 1.50
DateAgainLeft[Yes]	0.79	0.73 – 0.84
Gender[Female]	1.03	0.93 – 1.13
DateAgainRight[Yes]	1.32	1.24 – 1.41
DateAgainLeft[Yes]:Gender[Female]	1.03	0.96 – 1.11
Gender[Female]:DateAgainRight[Yes]	0.98	0.91 – 1.04
phi_DateAgainLeft[Yes]	1.16	1.05 – 1.29
phi_Gender[Female]	1.03	0.84 – 1.27
phi_DateAgainRight[Yes]	0.92	0.83 – 1.03
phi_DateAgainLeft[Yes]:Gender[Female]	0.98	0.88 – 1.08
phi_Gender[Female]:DateAgainRight[Yes]	0.88	0.79 – 0.97
zoi_DateAgainLeft[Yes]	0.73	0.52 – 1.03
zoi_Gender[Female]	1.03	0.49 – 2.15
zoi_DateAgainRight[Yes]	0.49	0.34 – 0.69
zoi_DateAgainLeft[Yes]:Gender[Female]	0.81	0.57 – 1.13
zoi_Gender[Female]:DateAgainRight[Yes]	1.27	0.89 – 1.79
coi_DateAgainLeft[Yes]	0.43	0.23 – 0.83
coi_Gender[Female]	0.85	0.42 – 1.89
coi_DateAgainRight[Yes]	3.18	1.67 – 6.18
coi_DateAgainLeft[Yes]:Gender[Female]	1.62	0.86 – 3.08
coi_Gender[Female]:DateAgainRight[Yes]	1.38	0.73 – 2.75
Random Effects		
σ^2	0.01	
$\tau_{00\ \text{Subject}}$	0.06	
N_{Subject}	35	
Observations	1009	

Notes: All predictors were sum-coded. Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Supplementary Table 9 - Model table for the Bayesian mixed model that predicts RT from Pre-date attractiveness ratings and Gender. This analysis was performed on the complete cases-dataset.

	RT	
Predictors	**Estimates**	**CI (95%)**
Intercept	1.19	-0.93 – 3.34
Gender[Female]	0.74	-1.49 – 2.92
AttractivenessDistractor	2.06	0.61 – 3.48
AttractivenessProbe	-1.11	-2.83 – 0.65
Gender[Female]: AttractivenessDistractor	-0.10	-1.52 – 1.28
Gender[Female]: AttractivenessProbe	2.06	0.28 – 3.79
Random Effects		
σ^2	2580.38	
$\tau_{00\ \mathrm{Subject}}$	2.29	
$\tau_{11\ \mathrm{Subject:AttractivenessDistractor}}$	5.24	
$\tau_{11\ \mathrm{Subject:AttractivenessProbe}}$	19.83	
N_{Subject}	55	
Observations	3198	

Notes: Gender was sum-coded, while Pre-date attractiveness ratings were centered around 4 (the middle option).

Supplementary Table 10 - Model table for the Bayesian mixed model that predicts RT from Post-date attractiveness ratings and Gender. This analysis was performed on the complete cases-dataset.

	RT	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.38	-1.38 – 2.19
Gender[Female]	-0.27	-2.19 – 1.63
AttractivenessDistractor	1.78	0.55 – 3.01
AttractivenessProbe	-0.91	-2.48 – 0.64
Gender[Female]: AttractivenessDistractor	0.46	-0.77 – 1.68
Gender[Female]: AttractivenessProbe	1.19	-0.38 – 2.75
Random Effects		
σ^2	2581.06	
$\tau_{00\ \mathrm{Subject}}$	1.30	
$\tau_{11\ \mathrm{Subject:AttractivenessDistractor}}$	1.73	
$\tau_{11\ \mathrm{Subject:AttractivenessProbe}}$	13.89	
N_{Subject}	55	
Observations	3198	

Notes: Gender was sum-coded, while Post-date attractiveness ratings were centered around 4 (the middle option).

Supplementary Table 11 - Model table for the Bayesian mixed model that predicts RT from Date outcome and Gender. This analysis was performed on the complete cases-dataset.

	RT	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.80	-1.19 – 2.77
Gender[Female]	1.01	-1.04 – 3.05
DateAgainProbe[yes]	-0.93	-3.31 – 1.35
DateAgainDistractor[yes]	1.97	0.01 – 3.97
Gender[Female]:DateAgainProbe[yes]	2.39	0.04 – 4.70
Gender[Female]:DateAgainDistractor[yes]	0.87	-1.14 – 2.86
Random Effects		
σ^2	2590.00	
$\tau_{00\ \text{Subject}}$	1.62	
$\tau_{11\ \text{Subject:DateAgainProbe[yes]}}$	26.86	
$\tau_{11\ \text{Subject:DateAgainDistractor[yes]}}$	4.46	
N_{Subject}	55	
Observations	3198	

Notes: All predictors were sum-coded.

Supplementary Table 12 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Pre-date attractiveness rating and Gender. This analysis was performed on the complete cases-dataset.

	Left bias	
Predictors	***Estimates***	***CI (95%)***
Intercept	0.95	0.88 – 1.03
phi_Intercept	5.64	4.55 – 7.03
zoi_Intercept	0.02	0.01 – 0.06
coi_Intercept	0.83	0.30 – 2.13
AttractivenessLeft	1.38	1.32 – 1.45
Gender[Female]	0.99	0.92 – 1.08
AttractivenessRight	0.70	0.67 – 0.72
AttractivenessLeft:Gender[Female]	1.00	0.95 – 1.04
Gender[Female]:AttractivenessRight	1.01	0.97 – 1.05
phi_AttractivenessLeft	0.95	0.87 – 1.04
phi_Gender[Female]	1.02	0.82 – 1.26
phi_AttractivenessRight	0.98	0.91 – 1.06
phi_AttractivenessLeft:Gender[Female]	0.98	0.90 – 1.07
phi_Gender[Female]:AttractivenessRight	1.07	1.00 – 1.16
zoi_AttractivenessLeft	1.13	0.89 – 1.44
zoi_Gender[Female]	1.04	0.51 – 2.11
zoi_AttractivenessRight	1.56	1.25 – 1.98
zoi_AttractivenessLeft:Gender[Female]	0.97	0.77 – 1.23
zoi_Gender[Female]:AttractivenessRight	0.83	0.65 – 1.04
coi_AttractivenessLeft	1.61	1.07 – 2.45
coi_Gender[Female]	0.83	0.42 – 1.77
coi_ AttractivenessRight	0.48	0.30 – 0.76
coi_AttractivenessLeft:Gender[Female]	0.84	0.56 – 1.32
coi_Gender[Female]:AttractivenessRight	1.22	0.77 – 2.00
Random Effects		
σ^2	0.01	
$\tau_{00\ \mathrm{Subject}}$	0.06	
N_{Subject}	35	
Observations	1009	

Notes: Gender was sum-coded, while Pre-date attractiveness ratings were centered around 4 (the middle option). Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Supplementary Table 13 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Post-date attractiveness rating and Gender. This analysis was performed on the complete cases-dataset.

	Left bias	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.93	0.85 – 1.01
phi_Intercept	4.49	3.62 – 5.53
zoi_Intercept	0.01	0.00 – 0.04
coi_Intercept	0.70	0.18 – 2.21
AttractivenessLeft	1.21	1.15 – 1.26
Gender[Female]	1.01	0.93 – 1.09
AttractivenessRight	0.79	0.75 – 0.82
AttractivenessLeft:Gender[Female]	0.98	0.94 – 1.02
Gender[Female]:AttractivenessRight	1.07	1.02 – 1.11
phi_AttractivenessLeft	0.90	0.84 – 0.97
phi_Gender[Female]	0.94	0.76 – 1.16
phi_AttractivenessRight	1.02	0.95 – 1.10
phi_AttractivenessLeft:Gender[Female]	1.03	0.95 – 1.10
phi_Gender[Female]:AttractivenessRight	1.00	0.93 – 1.07
zoi_AttractivenessLeft	1.26	0.99 – 1.63
zoi_Gender[Female]	1.09	0.51 – 2.31
zoi_AttractivenessRight	1.60	1.26 – 2.08
zoi_AttractivenessLeft:Gender[Female]	1.07	0.84 – 1.36
zoi_Gender[Female]:AttractivenessRight	0.79	0.61 – 1.00
coi_AttractivenessLeft	1.84	1.19 – 2.95
coi_Gender[Female]	0.98	0.46 – 2.23
coi_ AttractivenessRight	0.57	0.36 – 0.87
coi_AttractivenessLeft:Gender[Female]	0.88	0.56 – 1.45
coi_Gender[Female]:AttractivenessRight	1.14	0.73 – 1.80
Random Effects		
σ^2	0.01	
$\tau_{00\ \text{Subject}}$	0.06	
N_{Subject}	35	
Observations	1009	

Notes: Gender was sum-coded, while Post-date attractiveness ratings were centered around 4 (the middle option). Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Supplementary Table 14 - Model table for the Bayesian zero-one inflated beta regression predicting Looking time proportion to the left picture from Date outcome rating and Gender. This analysis was performed on the complete cases-dataset.

	Left bias	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.87	0.80 – 0.96
phi_Intercept	4.19	3.37 – 5.21
zoi_Intercept	0.02	0.00 – 0.06
coi_Intercept	0.58	0.19 – 1.52
DateAgainLeft[Yes]	1.27	1.19 – 1.36
Gender[Female]	1.03	0.94 – 1.13
DateAgainRight[Yes]	0.76	0.71 – 0.81
DateAgainLeft[Yes]:Gender[Female]	0.97	0.90 – 1.04
Gender[Female]:DateAgainRight[Yes]	1.03	0.96 – 1.09
phi_DateAgainLeft[Yes]	0.86	0.78 – 0.95
phi_Gender[Female]	1.03	0.83 – 1.28
phi_DateAgainRight[Yes]	1.08	0.98 – 1.21
phi_DateAgainLeft[Yes]:Gender[Female]	1.03	0.92 – 1.14
phi_Gender[Female]:DateAgainRight[Yes]	1.14	1.03 – 1.27
zoi_DateAgainLeft[Yes]	1.37	0.97 – 1.94
zoi_Gender[Female]	1.04	0.49 – 2.16
zoi_DateAgainRight[Yes]	2.04	1.45 – 2.96
zoi_DateAgainLeft[Yes]:Gender[Female]	1.24	0.88 – 1.76
zoi_Gender[Female]:DateAgainRight[Yes]	0.80	0.56 – 1.13
coi_DateAgainLeft[Yes]	2.34	1.22 – 4.46
coi_Gender[Female]	0.84	0.42 – 1.93
coi_DateAgainRight[Yes]	0.31	0.16 – 0.59
coi_DateAgainLeft[Yes]:Gender[Female]	0.62	0.32 – 1.16
coi_Gender[Female]:DateAgainRight[Yes]	0.72	0.37 – 1.35
Random Effects		
σ^2	0.01	
$\tau_{00\ \text{Subject}}$	0.06	
N_{Subject}	35	
Observations	1009	

Notes: All predictors were sum-coded. Estimates for the predictors were exponentiated, so that they represent Odds Ratios for the beta, coi and zoi parameters.

Appendix D: Supplementary Material for Chapter 6

Supplementary Table 1 - Model outputs for the Flange Size dot-probe.

	Kawan		Samboja		Sandy	
Predictors	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*
Intercept	-0.23	-9.95 – 9.36	-0.95	-10.69 – 8.64	-0.14	-9.80 – 9.68
Congruence [LargeFlanges]	-3.28	-19.79 – 13.37	3.90	-14.35 – 22.15	2.08	-15.99 – 19.99
ProbeLocation[Left]	5.08	-11.74 – 21.90	-6.61	-25.43 – 12.14	7.58	-10.45 – 25.68
Random Effects						
σ^2	178.89		301.29		258.61	
$\tau_{00\ \text{Session}}$	960.64		1735.80		2012.05	
Observations	133		131		140	

Note: all categorical independent variables were sum-to-zero coded.

Supplementary Table 2 - Model outputs for the Symmetry dot-probe.

	Kawan		Samboja		Sandy	
Predictors	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*
Intercept	-0.67	-10.29 – 8.90	-0.13	-9.87 – 9.54	-0.50	-10.16 – 9.31
Congruence [Symmetrical]	-2.10	-18.13 – 13.99	-3.82	-22.22 – 14.26	0.81	-17.21 – 18.90
ProbeLocation[Left]	12.09	-4.24 – 28.09	-7.11	-24.98 – 10.94	-1.11	-19.08 – 16.78
Random Effects						
σ^2	169.60		276.77		264.60	
$\tau_{00\ \text{Session}}$	2962.89		3146.86		4452.39	
Observations	152		142		154	

Note: all categorical independent variables were sum-to-zero coded.

Supplementary Table 3 - Model output for the Flange Size preference test.

	Preference	
Predictors	*Odds Ratios*	*CI (95%)*
Intercept	1.00	0.73 – 1.38
Color Flanged[Green]	0.67	0.52 – 0.91
Order[FlangedRedFirst]	0.88	0.67 – 1.18
Random Effects		
$\tau_{00\ \mathrm{Subject}}$	0.11	
$\tau_{00\ \mathrm{Subject:Session}}$	0.01	
$\tau_{11\ \mathrm{Subject:Color\ Flanged}}$	0.09	
$N_{\mathrm{SubjectName}}$	6	
Observations	570	

Note: all categorical independent variables were sum-to-zero coded.

Supplementary Table 4 - Model output for the Flange Size preference test, including vertical location.

	Preference	
Predictors	*Odds Ratios*	*CI (95%)*
Intercept	1.00	0.74 – 1.35
Color Flanged[Green]	0.65	0.49 – 0.90
Order[FlangedRedFirst]	0.86	0.65 – 1.15
Vertical_Location	16.97	9.35 – 30.66
Random Effects		
$\tau_{00\ \mathrm{Subject}}$	0.27	
$\tau_{00\ \mathrm{Subject:Session}}$	0.13	
$\tau_{11\ \mathrm{Subject:Color\ Flanged}}$	0.26	
$N_{\mathrm{SubjectName}}$	6	
Observations	570	

Note: all categorical independent variables were sum-to-zero coded. Continuous independent variable Vertical_Location was centralized around 0.5.

Appendix E: Supplementary Material for Chapter 7

Supplementary Table 1 – Model tables for the binary logistic regressions that predict first fixation on flanged males for Experiment 1 and 2.

Predictors	**Experiment 1**		**Experiment 2**	
	First Fixation Flanged		**First Fixation Flanged**	
	Odds Ratios	*CI (95%)*	*Odds Ratios*	*CI (95%)*
Intercept	1.54	0.63 – 3.30	1.40	0.77 – 2.41
FlangedLocation[Left]	2.14	1.57 – 2.99	1.51	1.11 – 2.07
Random Effects				
Intercept$_{\text{Participant}}$	0.74		0.38	
Intercept$_{\text{Participant:Session}}$	0.24		0.51	
N $_{\text{Session}}$	45		70	
N $_{\text{Participant}}$	4		4	
Observations	195		186	

Note: Predictors were sum-coded.

Supplementary Table 2 – Model tables for the zero-one inflated beta regressions that predict looking time bias to flanged males for Experiment 1 and 2.

	Experiment 1		**Experiment 2**	
	Looking time bias		**Looking time bias**	
Predictors	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*
Intercept	1.09	0.72 – 1.59	1.29	0.89 – 1.83
phi_Intercept	4.07	1.78 – 8.18	4.36	2.44 – 7.43
zoi_Intercept	0.31	0.13 – 0.94	0.39	0.11 – 1.74
coi_Intercept	2.82	0.57 – 11.36	2.91	0.83 – 12.12
FlangedLocation[Left]	0.99	0.84 – 1.17	0.93	0.79 – 1.10
phi_FlangedLocation[Left]	0.96	0.74 – 1.24	1.25	0.96 – 1.62
zoi_FlangedLocation[Left]	1.23	0.88 – 1.73	0.88	0.60 – 1.26
coi_FlangedLocation[Left]	1.31	0.64 – 2.72	1.39	0.69 – 2.85
Random Effects				
Intercept$_{\text{Participant}}$	0.26		0.24	
phi_Intercept$_{\text{Participant}}$	0.55		0.36	
zoi_Intercept$_{\text{Participant}}$	0.73		1.35	
coi_Intercept$_{\text{Participant}}$	1.25		0.79	
Intercept$_{\text{Participant:Session}}$	0.21		0.19	
phi_Intercept$_{\text{Participant:Session}}$	0.27		0.30	
zoi_Intercept$_{\text{Participant:Session}}$	0.53		0.87	
coi_Intercept$_{\text{Participant:Session}}$	0.55		1.44	
N $_{\text{Session}}$	44		70	
N $_{\text{Participant}}$	4		4	
Observations	195			

Note: Predictors were sum-coded.

Supplementary Table 3 – Model table for the binary logistic regression that predicts first fixation to the left as a function of male morph on the left and right side of the screen.

	First Fixation Left	
Predictors	*Odds Ratios*	*CI (95%)*
Intercept	1.46	0.35 – 5.29
Morph Left [Flanged]	1.19	0.88 – 1.61
Morph Right [Flanged]	0.74	0.54 – 1.01
Morph Left [Flanged]: Morph Right [Flanged]	1.01	0.74 – 1.38
Random Effects		
Intercept$_{\text{Participant}}$	1.89	
Intercept$_{\text{Participant:Session}}$	0.43	
N$_{\text{Session}}$	71	
N$_{\text{Participant}}$	4	
Observations	274	

Note: Predictors were sum-coded.

Supplementary Table 4 - Model table for the zero-one inflated beta regression that predicts total attention to the left as a function of male morph on the left and right side of the screen.

	Looking time bias left	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.93	0.45 – 1.93
phi_Intercept	5.07	3.07 – 7.95
zoi_Intercept	0.42	0.13 – 1.77
coi_Intercept	1.81	0.17 – 19.01
Morph Left [Flanged]	1.15	1.00 – 1.31
Morph Right [Flanged]	0.84	0.73 – 0.96
Morph Left [Flanged]: Morph Right [Flanged]	1.00	0.87 – 1.15
phi_Morph Left [Flanged]	1.09	0.86 – 1.37
phi_Morph Right [Flanged]	0.87	0.69 – 1.08
phi_Morph Left [Flanged]: Morph Right [Flanged]	0.97	0.76 – 1.26
zoi_Morph Left [Flanged]	0.97	0.72 – 1.30
zoi_Morph Right [Flanged]	1.08	0.80 – 1.45
zoi_Morph Left [Flanged]: Morph Right [Flanged]	1.02	0.75 – 1.36
coi_Morph Left [Flanged]	2.74	1.21 – 6.94
coi_Morph Right [Flanged]	0.75	0.33 – 1.66
coi_Morph Left [Flanged]: Morph Right [Flanged]	1.12	0.49 – 2.61
Random Effects		
Intercept$_{\text{Participant}}$	0.69	
phi_Intercept$_{\text{Participant}}$	0.27	
zoi_Intercept$_{\text{Participant}}$	1.30	
coi_Intercept$_{\text{Participant}}$	3.37	
Intercept$_{\text{Participant:Session}}$	0.26	
phi_Intercept$_{\text{Participant:Session}}$	0.27	
zoi_Intercept$_{\text{Participant:Session}}$	0.32	
coi_Intercept$_{\text{Participant:Session}}$	1.29	
N$_{\text{Session}}$	71	
N$_{\text{Participant}}$	4	
Observations	274	

Note: Predictors were sum-coded.

Supplementary Table 5 – Pairwise contrasts for each combination of stimuli for (I) the binary logistic regression that predicts first fixation to the left and (II) the zero-one inflated beta regression that predicts total attention to the left as a function of male morph on the left and right side of the screen.

Contrast		First fixation (binary logistic regression)			Total attention (zero-one inflated beta regression)		
		Median estimate	89% credible interval	Probability of direction	Median estimate	89% credible interval	Probability of direction
FM-FM	FM-UFM	-0.064	-0.140; 0.012	0.908	-0.064	-0.140; 0.012	0.908
FM-FM	UFM-FM	0.101	0.027; 0.179	0.988	0.101	0.027; 0.179	0.988
FM-FM	UFM-UFM	0.023	-0.060; 0.111	0.675	0.023	-0.060; 0.111	0.675
FM-UFM	UFM-UFM	0.088	0.013; 0.164	0.970	0.088	0.013; 0.164	0.970
UFM-FM	FM-UFM	-0.165	-0.227; -0.104	1.000	-0.165	-0.227; -0.104	1.000
UFM-FM	UFM-UFM	-0.077	-0.151; -0.005	0.958	-0.077	-0.151; -0.005	0.958

Supplementary Table 6 - Model tables for the zero-one inflated beta regressions that predict total attention to specific male individuals per female participant.

	Samboja		Sandy		Wattana	
Predictors	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*	*Estimates*	*CI (95%)*
Intercept	1.00	0.84 – 1.19	1.00	0.83 – 1.21	1.00	0.81 – 1.23
phi_Intercept	4.45	3.19 – 6.45	4.87	2.83 – 8.52	4.75	3.29 – 6.94
zoi_Intercept	0.20	0.08 – 0.38	0.91	0.43 – 1.93	0.84	0.44 – 1.64
coi_Intercept	1.00	0.39 – 2.60	1.00	0.57 – 1.76	1.00	0.56 – 1.79
focus[Bako]	1.14	0.83 – 1.54	1.27	0.92 – 1.75	1.39	0.97 – 1.95
focus[Jingga]	0.83	0.62 – 1.11	1.04	0.77 – 1.44	0.98	0.67 – 1.44
focus[Sibu]	1.14	0.85 – 1.53	0.78	0.54 – 1.15	0.93	0.66 – 1.32
distractor[Bako]	0.88	0.65 – 1.20	0.79	0.58 – 1.08	0.72	0.51 – 1.01
distractor[Jingga]	1.21	0.90 – 1.62	0.95	0.70 – 1.29	1.02	0.69 – 1.49
distractor[Sibu]	0.87	0.66 – 1.18	1.28	0.87 – 1.85	1.07	0.76 – 1.50
phi_focus[Bako]	0.72	0.44 – 1.15	1.00	0.54 – 1.83	1.39	0.77 – 2.46
phi_focus[Jingga]	0.76	0.46 – 1.28	1.94	0.97 – 3.81	0.59	0.34 – 1.01
phi_focus[Sibu]	0.88	0.54 – 1.43	0.62	0.34 – 1.15	1.44	0.82 – 2.47
phi_distractor[Bako]	0.71	0.43 – 1.16	1.00	0.53 – 1.85	1.40	0.77 – 2.46
phi_distractor[Jingga]	0.77	0.46 – 1.30	1.95	0.97 – 3.77	0.59	0.34 – 1.01
phi_distractor[Sibu]	0.88	0.55 – 1.43	0.62	0.33 – 1.14	1.44	0.82 – 2.45
zoi_focus[Bako]	0.72	0.31 – 1.58	1.16	0.60 – 2.30	1.36	0.72 – 2.63
zoi_focus[Jingga]	1.39	0.63 – 2.99	1.61	0.81 – 3.30	1.02	0.52 – 1.97
zoi_focus[Sibu]	1.09	0.48 – 2.38	1.16	0.58 – 2.31	0.94	0.48 – 1.84
zoi_distractor[Bako]	0.72	0.31 – 1.55	1.17	0.59 – 2.27	1.37	0.71 – 2.67
zoi_distractor[Jingga]	1.38	0.62 – 2.98	1.61	0.82 – 3.22	1.02	0.52 – 1.96
zoi_distractor[Sibu]	1.08	0.48 – 2.38	1.16	0.58 – 2.30	0.94	0.48 – 1.80
coi_focus[Bako]	0.81	0.22 – 2.91	1.74	0.76 – 4.14	1.21	0.50 – 2.91
coi_focus[Jingga]	0.53	0.15 – 1.78	0.73	0.31 – 1.70	1.26	0.53 – 3.10
coi_focus[Sibu]	2.44	0.72 – 8.90	1.52	0.66 – 3.64	1.36	0.56 – 3.30
coi_distractor[Bako]	1.23	0.35 – 4.46	0.57	0.24 – 1.31	0.83	0.35 – 1.98
coi_distractor[Jingga]	1.87	0.56 – 6.41	1.36	0.59 – 3.23	0.79	0.32 – 1.90
coi_distractor[Sibu]	0.42	0.11 – 1.38	0.66	0.27 – 1.53	0.74	0.30 – 1.79
Random Effects						
Intercept$_{Session}$	0.07		0.09		0.09	
phi_Intercept$_{Session}$	0.39		0.81		0.26	
zoi_Intercept$_{Session}$	1.05		1.34		1.05	
coi_Intercept$_{Session}$	0.46		0.26		0.27	
N$_{Session}$	20		17		18	
Observations	134		142		134	

Note: Predictors were sum-coded.

Supplementary Table 7 – Pairwise contrasts for the zero-one inflated beta regressions that predict total attention to specific male individuals per female participant. Pd = probability of direction.

Contrast		Samboja			Sandy			Wattana		
		Median estimate	**89% credible interval**	***pd***	**Median estimate**	**89% credible interval**	***pd***	**Median estimate**	**89% credible interval**	***pd***
Bako	Jingga	0.084	-0.019; 0.186	0.905	0.123	-0.008; 0.254	0.931	0.038	-0.097; 0.177	0.668
Bako	Sibu	-0.043	-0.147; 0.057	0.749	0.073	-0.055; 0.209	0.806	0.038	-0.095; 0.174	0.672
Bako	Wousan	0.034	-0.073; 0.142	0.696	0.142	0.0148; 0.265	0.964	0.156	0.011; 0.294	0.960
Jingga	Sibu	-0.127	-0.228; -0.024	0.976	-0.051	-0.185; 0.092	0.715	0.001	-0.137; 0.131	0.502
Jingga	Wousan	-0.050	-0.160; 0.057	0.772	0.018	-0.112; 0.152	0.586	0.121	-0.013; 0.261	0.916
Sibu	Wousan	0.077	-0.029; 0.182	0.879	0.068	-0.054; 0.200	0.808	0.119	-0.009; 0.254	0.925

Appendix F: Supplementary Material for Chapter 8

Supplementary Table 1 – Orang-utans housed at Allwetter Zoo during the study periods.

Name	Sex	Date of Birth
Temmy	*F*	*07-12-1981*
Sari	F	26-07-1970
Mandi	F	19-12-1999
Niah	F	08-05-2013
Mr. Miyagi	M	05-05-2014
Ramon (only 2nd study period)	M	20-11-1998

Appendix G: model stability checks

In this appendix, I strive to provide extra information about the model checks that I performed across the empirical chapters in order to assess model stability. First, I will give some context with regard to the WAMBS-checklist (Depaoli & van der Schoot, 2017) that was used to test for model convergence issues throughout the thesis, posterior predictive checks based on the posterior distribution and cross-validation, and Pareto smoothed importance sampling for identification of influential cases (Vehtari et al., 2017). Second, I will provide posterior predictive checks and diagnostics about influential observations for each empirical chapter.

Model convergence

While relatively simple Bayesian models can rely on methods like grid approximation to estimate the posterior distribution, such methods quickly become computationally costly in the context of multidimensional models that require the approximation of joint posterior distributions (Kruschke, 2014; Johnson et al., 2022). One solution that has gained traction is the use of algorithms such as MCMC (Markov chain Monte Carlo) sampling. Such algorithms provide a useful tool to approximate complex multidimensional posterior distributions rather efficiently by generating values from the posterior distribution via randomly 'walking' through the parameter space combined with simple decision rules (Kruschke, 2014). Johnsen et al. (2022) provide an excellent explanation of and tutorial on MCMC sampling.

Although MCMC algorithms have provided most useful for Bayesian inference, their usefulness depends strongly on the accuracy and stability of the process. Therefore, it is essential to throughly examine the posterior samples and the stochastics of the algorithm. The WAMBS checklist (Depaoli & van der Schoot, 2017) provides some useful criteria to evaluate these sources of information. First, one can check whether the models converged properly by visually evaluating the trace plots for all four chains for all parameters in the model. By visually inspecting the plots, it is possible to identify divergent transitions, slow mixing within a chain, or chains getting stuck on one particular value. All these issues can result in poor approximation of the posterior distribution (Johnsen et al., 2022). Second, one can visually check the autocorrelation between consecutive iterations within a chain. Although consecutive iterations are by definition autocorrelated to some extent, extreme degrees of autocorrelation can indicate estimation problems within the model (Depaoli & van der Schoot, 2017). Third, one can visually check the histograms of the posterior distributions for each parameter for gaps or other abnormalities. In most cases, the posterior distributions are expected to be smooth and follow a Gaussian distribution, with one exception being variance parameters that are zero-bounded. Fourth, to investigate the similarity between separate chains, one can examine the Gelman-Rubin statistic (Gelman & Rubin, 1992). This statistic compares the within-chain variability to the between-chain variability. If between-chain variance is relatively small compared to within-chain variance -which is indicative of a well-converged model- the Gelman-Rubin diagnostic for a parameter should be close to 1, and at least not larger than 1.1 (Gelman & Rubin, 1992). The *brms*-package incorporates an adapted version of the Gelman-Rubin diagnostic, that is reported as the Rhat (Vehtari et al., 2021).

For all Bayesian regression models reported in this thesis, the above-mentioned steps were taken to ensure correct convergence of the models. I identified no convergence issues in any of the models reported. Therefore, in the remainder of this appendix, I will not report the specific diagnostics per model.

Posterior predictive checks

Next to convergence, there are other aspects of Bayesian regression models that are important to check, such as the predictive validity of the model. If a model fits well to the data, it should be able to predict new data from this model that are relatively similar to our original data (Johnsen et al., 2022; Kruschke, 2014). It is important to note that this is a different question from model convergence: a well-converged model can have a poor fit to the underlying data. For example, one can easily fit a converging Gaussian regression model to extremely zero-inflated data, and -despite the convergence- predictions based on the model will deviate strongly from the underlying data, indicating model misspecification.

One way to test whether the model fits the original data well is performing visual checks of the posterior predictive distribution. This can be done by creating graphs that plot the distribution of the original data on top of the distributions based on multiple simulated datasets randomly drawn from the posterior predictive distribution (Gabry et al., 2019). If the model fits the original data well, we expect the distribution of the original data to overlap with the distributions of simulated datasets. However, if this is not the case, the model is potentially misspecified, either because important predictors are missing or because the error distribution of the model does not fit the data well (Johnsen et al., 2022). Therefore, I will report posterior predictive checks for the main models reported in the empirical chapters.

Pareto smoothed importance sampling (PSIS)

One important aspect of checking model stability is to investigate whether there are multivariate outliers that strongly influence the posterior distribution. If many of such observations are present, this might indicate that the model is biased. In Bayesian regression models, such influential cases can be identified using Pareto smoothed importance sampling combined with LOO cross-validation (Vehtari et al., 2017). With this approach, for every removed observation, a Pareto distribution is fitted to the 20% largest importance ratios. Based on this process, a k-value (the shape parameter of the Pareto distibution) can be calculated, which indicates whether an observation is influential. In general, k-values up to 0.7 suggest that the observation is not overly influential, while estimates above 1 are indicative of strongly influential observations. If multiple observations have k-values > 0.7, but especially > 1, this might indicate issues with the model fit. It is important to note, though, that no threshold exists for how many high k-values are acceptable: a small number of high k-values is not problematic per se. I will report whether there were any influential observations found for the main models reported in the empirical chapters.

Chapter 3

Posterior predictive check

Posterior predictive checks based on the posterior predictive distribution indicated good model fit (Figure 1)

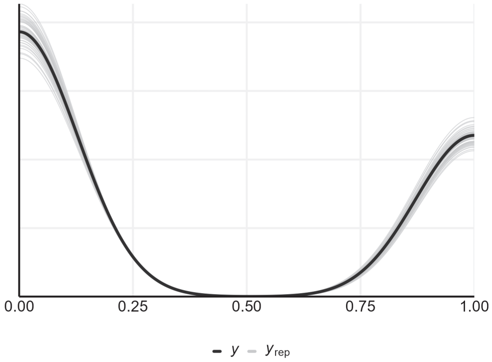


Figure 1 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black).

PSIS

Only one out of 457 observations had a k-value just over 0.7, indicating that this observation had relatively large effect on the posterior distribution. However, because it concerned only one observation, it is unlikely to heavily influence model stability.

Chapter 4

Posterior predictive check

Posterior predictive checks based on the posterior predictive distribution indicated good model fit for all three experiments (Figure 2).

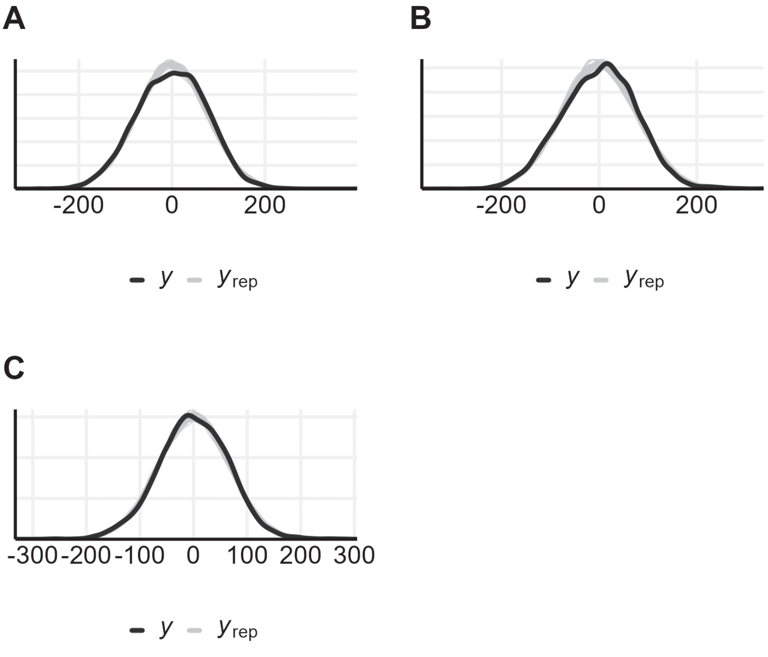


Figure 2 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black) for (A) Experiment 1, (B) Experiment 2, and (C) Experiment 3.

PSIS

For the three main models, all k-values were < 0.5, indicating that no extremely influential observations were found.

Chapter 5

Dot-probe

Posterior predictive check

For both dot-probe models the posterior predictive distribution indicated that the models were able to predict the data accurately, although the original data distribution appears slightly more narrow than the simlated distributions (Figure 3).

For both models eye-tracking models, the posterior predictive distributions slightly deviate from the original data distribution. This is very likely caused by the beta distribution that does not fit well to multimodal distributions, such as the distribution of the original data. However, solving this issue would entail specifying a custom distribution that covers both the zero-one inflation part as well as the multimodal beta distribution. Currently, no such distribution is available. This, combined with the absence of further issues related to convergence with the models, has led me to retain the models as they are (Figure 3).

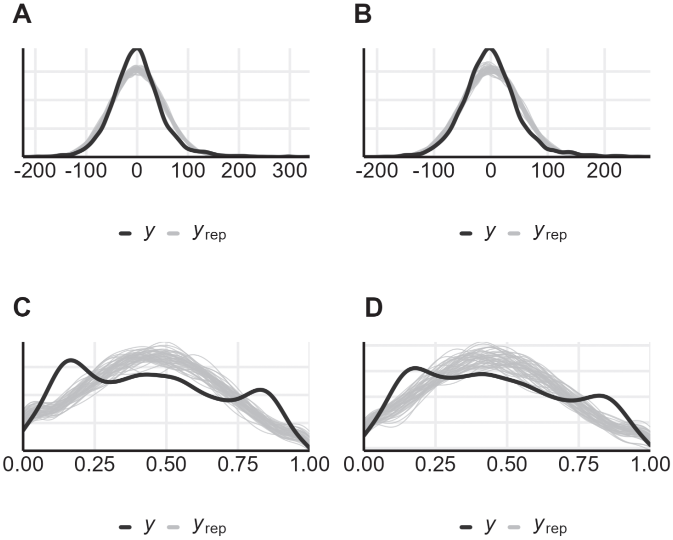


Figure 3 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black) for (A) dot-probe with attractiveness ratings, (B) dot-probe with date outcome 2, (C) eye-tracking with attractiveness ratings, and (D) eye-tracking with date outcome.

PSIS

For both dot-probe models, all k-values were < 0.5, indicating that no extremely influential observations were found. For the attractiveness rating model, only one out of 1569 observations had a k-value just over 0.7, indicating that this observation had relatively large effect on the posterior distribution. However, because it concerned only one observation, it is unlikely to heavily influence model stability. For the date response model, four out of 1009 observations yielded k-values > 0.7. To ensure model stability, I ran the model without these four observations included, which resulted in the same quantitative results as the original model.

Chapter 6

Posterior predictive check

For all models, both the individual dot-probe models (Figure 4) and the preference test model (Figure 5), posterior predictive checks showed no indication of model misspecification.

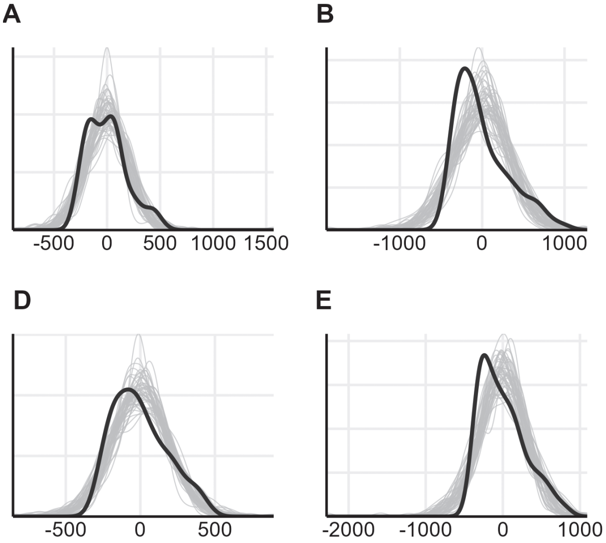


Figure 4 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black) for the flange size dot-probe separately for (A) Kawan, (B) Samboja, and (C) Sandy; for the symmetry dot-probe separately for (D) Kawan, (E) Samboja, and (F) Sandy.

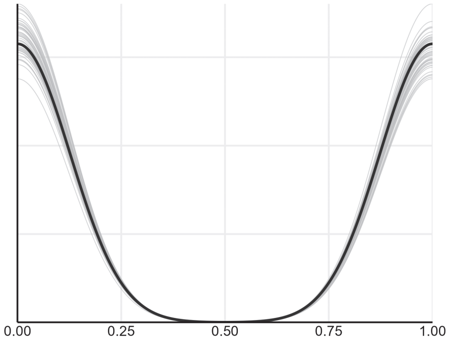


Figure 5 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black) for the preference test model.

PSIS

For all dot-probe models and the preference test model, all k-values were < 0.5, indicating that no extremely influential observations were found.

Chapter 7

Experiment 1

Posterior predictive check

For experiment 1, posterior predictive checks showed no indication of model misspecification for both the first fixation- and the total fixation duration-model. For experiment 2, posterior predictive checks showed no indiviation of model misspecifications for the first fixation- and the total fixation duration-models (Figure 6).

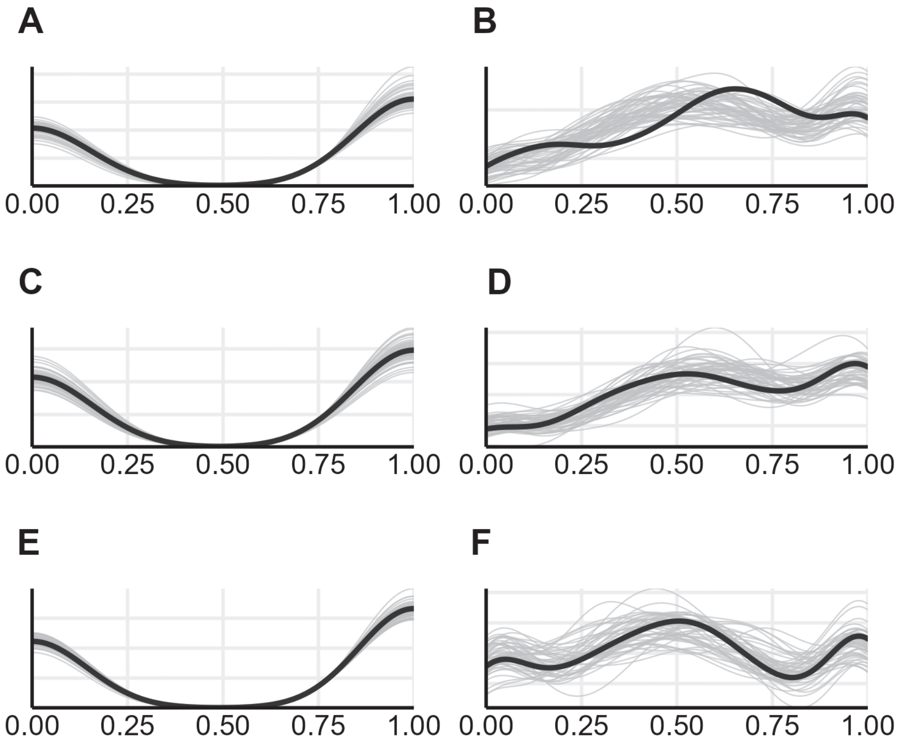


Figure 6 – Predictive posterior distribution of 50 simulated datasets based on the model (in grey) with the distribution of the original data plotted on top (in black) for experiment 1: (A) first fixation model, (B) total fixation duration model; experiment 2: (C) first fixation model replicating exp. 1, (D) total fixation duration model replicating exp. 1, (E) second first fixation duration model, and (F) second total fixation duration model.

PSIS

For experiment 1, all k-values were < 0.7 for the first fixation-model. For the total fixation duration-model, three of 195 observations had a k > 0.7, indicating that they had a strong influence on the posterior. However, after refitting the model without these observations, the main result remained the same.

For experiment 2, all k-values were < 0.7 for the first fixation-model that replicated experiment 1. For the total fixation duration-model that replicated experiment 1, six of 186 observations had a k > 0.7, indicating that they had a strong influence on the posterior. However, after refitting the model without these observations, the main result remained the same. For the second first fixation-model, all k-values were < 0.7. For the second total fixation duration-model that replicated experiment 1, five of 274 observations had a k > 0.7, indicating that they had a strong influence on the posterior. However, after refitting the model without these observations, the main result remained the same.

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Samenvatting

Als mensen spreken over hun geliefde gebruiken ze vaak cognitieve termen: “ze trok meteen mijn aandacht” of “ik kon hem niet uit mijn hoofd krijgen” zijn veelgehoorde uitspraken als het over romantische interacties bij mensen gaat. Het wordt dan ook algemeen geaccepteerd dat cognitieve processen ons helpen bij het kiezen van een partner. Bij dieren is echter veel minder bekend over de rol van cognitie bij partnerkeuze. Dit is zonde, omdat onderzoek hiernaar zowel fundamentele als toegepaste waarde heeft. Naast het feit dat vergelijkend onderzoek naar cognitie en partnerkeuze ons inzicht geeft in de evolutionaire oorsprong van hoe mensen hun partner kiezen, kunnen we de onderzoeksmethoden ook toepassen om partnervoorkeuren van dieren inzichtelijk te maken. Internationaal zijn er voor verschillende diersoorten fokprogramma’s opgezet die moeten zorgen voor een genetisch gezonde dierentuinpopulatie. Momenteel worden individuele partnervoorkeuren van dieren daarin nog nauwelijks meegenomen. Door dit wel te doen, kan het reproductief succes van dierentuinpopulaties mogelijk verhoogd worden. In mijn onderzoek heb ik daarom geprobeerd om cognitieve experimenten te ontwerpen die inzicht kunnen geven in de partnervoorkeuren van orang-oetans, een mensaapsoort die nauw verwant is aan de mens en in dierentuinen een relatief laag reproductief succes kent. Dit heb ik gedaan door een vergelijkende benadering toe te passen, waarbij mensen en orang-oetans dezelfde soort experimenten uitvoerden.

Na een algemene inleiding in **hoofdstuk 1**, geef ik in **hoofdstuk 2** een overzicht van eerder onderzoek naar cognitie en partnerkeuze bij mensen en niet-menselijke primaten. Hierbij belicht ik drie specifieke componenten: aandacht, geheugen en inspanning. Bij mensen is uitgebreid onderzoek gedaan naar deze componenten, waarbij bevindingen aantonen dat mensen (i) hun visuele aandacht reflexief en bewust op aantrekkelijke gezichten richten, (ii) bereid zijn moeite te doen om aantrekkelijke gezichten te zien, en (iii) mogelijk een beter geheugen hebben voor aantrekkelijke gezichten dan onaantrekkelijke gezichten, hoewel sommige studies een beter geheugen voor onaantrekkelijke gezichten rapporteren. Ondanks het feit dat er in de laatste decennia steeds meer cognitieve experimenten met niet-menselijke primaten zijn uitgevoerd, is er nog maar weinig onderzoek gedaan naar cognitie en partnerkeuze. De meeste cognitiestudies gebruikten taken om kijkvoorkeuren te meten en waren voornamelijk gericht op makaken. Om een beter inzicht te krijgen in de evolutionaire geschiedenis van cognitieve processen die mensen tijdens partnerkeuze gebruiken, is het essentieel om een breder scala aan cognitieve taken toe te passen bij verschillende primatensoorten. Dit zou niet alleen onze eigen evolutionaire geschiedenis kunnen verhelderen, maar ook een meer praktische waarde kunnen hebben. Als deze taken namelijk inzicht kunnen geven in de partnerkeuze van individuen, zouden ze kunnen worden gebruikt binnen fokprogramma's om de ideale partner voor een individu te vinden.

De volgende drie hoofdstukken richten zich specifiek op partnerkeuze bij mensen. In **hoofdstuk 3** beschrijf ik hoe verschillende modaliteiten van aantrekkelijkheid invloed hebben op partnerkeuze tijdens een speed-date experiment. Recent onderzoek suggereert namelijk dat geur en geluid mogelijk veel belangrijker zijn voor partnerkeuze dan vaak wordt gedacht, maar empirisch onderzoek hiernaar is nog schaars. Van alle deelnemers aan ons onderzoek verzamelden we een portretfoto, een gestandaardiseerde opname van hun stem, en een recent gedragen T-shirt. Vervolgens lieten we alle deelnemers de visuele, auditieve en olfactorische aantrekkelijkheid van de deelnemers van het andere geslacht beoordelen. Daarna gingen alle deelnemers met elkaar op korte speed-dates en gaven per date aan of ze deze voor herhaling vatbaar vonden. De resultaten lieten zien dat met name visuele aantrekkelijkheid een goede voorspeller was van date succes: als een deelnemer iemands foto als aantrekkelijk had beoordeeld, was de kans ook groter dat die deelnemer de date voor herhaling vatbaar vond. Dit was minder tot niet het geval voor auditieve of olfactorische aantrekkelijkheid. Kortom, het lijkt erop dat mensen tijdens eerste interacties met potentiële romantische partners sterk op visuele informatie afgaan, en niet zozeer op geur en geluid.

In **hoofdstuk 4** heb ik bij bezoekers van dierenpark Apenheul onderzocht hoe aantrekkelijkheid en gezichtssymmetrie onze directe aandacht beïnvloeden. Daarnaast onderzocht ik ook of mensen automatisch de kijkrichting van aantrekkelijke gezichten volgen. Om de invloed van aantrekkelijkheid op aandacht te onderzoeken, hebben we de zogenaamde *dot-probe taak* gebruikt. Tijdens deze taak kregen deelnemers telkens twee portretfoto's van mensen van het andere geslacht voor een héél korte tijd te zien, waarvan er ééntje werd vervangen door een zwarte stip waar de deelnemer op moest klikken. Hoe sneller de deelnemers reageerden, hoe meer hun aandacht getrokken werd door de foto die vervangen werd door de stip. De foto's waren in eerder onderzoek beoordeeld door een andere groep mensen, en op basis daarvan verdeeld in aantrekkelijke, gemiddelde en onaantrekkelijke gezichten. Uit onze resultaten bleek dat mensen, ongeacht hun leeftijd of geslacht, sneller reageerden op aantrekkelijke foto's, wat laat zien dat hun aandacht direct uitging naar aantrekkelijke gezichten.

Dit was echter niet het geval toen we hetzelfde experiment herhaalden met symmetrische en asymmetrische gezichten: de deelnemers reageerden even snel op beide typen foto's. Dit resultaat suggereert dat mensen niet meteen hun aandacht vestigen op symmetrische gezichten. Daarnaast vonden we in het derde experiment geen invloed van aantrekkelijkheid op het volgen van kijkrichting: deelnemers volgden automatisch de kijkrichting van de foto's die we ze lieten zien, onafhankelijk van de aantrekkelijkheid van de persoon op de foto. Waarschijnlijk speelt aantrekkelijkheid dus nauwelijks een rol bij het automatisch imiteren van kijkrichting.

Hoewel hoofdstuk 4 al liet zien dat mensen automatisch hun aandacht focussen op aantrekkelijke gezichten, onderzocht ik dit in **hoofdstuk 5** in meer detail door ook naar vrijwillige aandacht te kijken én deze aandachtsvoorkeuren te linken aan partnerkeuze. Hiervoor voerden we een speed-date experiment uit, dat we combineerden met twee cognitieve taken. De resultaten op het gebied van directe, automatische aandacht waren ietwat afwijkend van de resultaten in hoofdstuk 4, omdat we in dit geval alleen een duidelijk effect vonden bij mannelijke deelnemers: zij reageerden sneller wanneer de stip een foto van een vrouw verving die zij als aantrekkelijk hadden beoordeeld. Om vrijwillige aandacht te meten lieten we deelnemers telkens gedurende vier seconden twee foto's zien, en bepaalden we door middel van *eye-tracking* hun kijkrichting gedurende deze periode. Op het gebied van vrijwillige aandacht zagen we dat zowel mannelijke als vrouwelijke deelnemers veel langer keken naar het gezicht dat zij aantrekkelijker vonden. Daarnaast was dit ook voorspellend voor hun partnerkeuze tijdens het speed-daten: deelnemers keken langer naar foto's van mensen waarmee ze later een succesvolle date hadden. Mogelijk komt dit omdat zowel de kijkrichting en de uiteindelijke partnerkeuze sterk afhankelijk zijn van aantrekkelijkheid. Al met al laat dit hoofdstuk zien dat met name vrijwillige aandacht, maar tot op zekere hoogte ook directe aandacht, een indicator is van partnervoorkeuren.

De drie volgende hoofdstukken gaan specifiek over Borneo orang-oetans. Deze mensaapsoort leeft semi-solitair en wordt gekenmerkt door het feit dat er twee verschillende typen volwassen mannetjes zijn. Allereerst zijn er de mannen met wangplaten: zij zijn twee keer zo groot als vrouwtjes, hebben grote wangplaten aan de zijkant van hun gezicht, en produceren *long calls*, luide vocalisaties die vanaf meer dan 1km afstand te horen zijn. Daarnaast zijn er mannen zonder wangplaten, die wel seksueel actief zijn, maar qua uiterlijk erg lijken op volwassen vrouwtjes. De vrouwtjes hebben een duidelijke partnervoorkeur voor mannen mét wangplaten. Omdat het voortplantingssucces van orang-oetans in dierentuinen relatief laag is, heb ik geprobeerd om experimenten te ontwikkelen die inzicht kunnen geven in de partnervoorkeuren van orang-oetans, zodat deze voorkeuren kunnen worden meegenomen in het Europese fokprogramma.

In **hoofdstuk 6** heb ik twee *touchscreen*-taken gebruikt om inzicht te krijgen in de aandachtsvoorkeuren van orang-oetans. Ten eerste gebruikte ik de *dot-probe taak,* die ik in hoofdstuk 4 en 5 ook bij mensen toepaste, om te bepalen of orang-oetans hun aandacht direct focussen op foto's van orang-oetan mannen met grote wangplaten of symmetrische gezichten. Dit was echter niet het geval. Daarnaast voerde ik een keuzetaak uit, waarbij de orang-oetans zelf konden kiezen of ze een foto van een man mét of zónder wangplaten wilden zien door op een rode of groene stip te klikken. De verwachting was dat ze liever foto's van mannen met wangplaten zouden willen zien, maar alle orang-oetans hadden geen voorkeur en kozen 50/50 voor foto's met en zonder wangplaten. Wél bleek in deze taak dat er een aantal andere factoren waren die hun selectie beïnvloedde. Zo leken de orang-oetans bijvoorbeeld energie te besparen door meestal de categorie te selecteren waarvoor ze hun arm het minst hoefde op te tillen, en leken ze een voorkeur te hebben voor de rode stip. Het lijkt er dus op dat andere factoren een grotere invloed hadden op hun keuze dan het type foto dat ze te zien zouden krijgen.

In **hoofdstuk 7** heb ik gebruik gemaakt van *eye tracking* bij de orang-oetans om zowel directe als vrijwillige aandacht te onderzoeken. Net als ik in hoofdstuk 5 deed met menselijke deelnemers, liet ik de orang-oetans telkens twee foto's zien gedurende vier seconden en bepaalde met een *eye tracker* waar ze naar keken. In het eerste experiment kregen ze telkens één foto van een man met wangplaten en één foto van een man zonder wangplaten te zien. De orang-oetans hadden een voorkeur voor foto's van mannen mét wangplaten, zowel in directe als vrijwillige aandacht. In een tweede experiment liet ik ze foto's zien van vier specifieke orang-oetan mannen, twee met en twee zonder wangplaten, in alle mogelijke combinaties. De resultaten van het experiment lieten zien dat -net als in experiment 1- de aandacht met name uitging naar foto's van mannen met wangplaten. We vonden echter geen uitgesproken voorkeuren voor een bepaald individu. Mogelijk komt dit doordat hiervoor meer datapunten nodig zijn. Al met al kunnen we dus concluderen dat orang-oetans hun aandacht focussen op mannen met wangplaten. De vraag blijft echter of ze dit doen uit positieve interesse of uit waakzaamheid.

Omdat orang-oetan mannen veel gebruik maken van auditieve communicatie, heb ik in **hoofdstuk 8** gefocust op de perceptie en productie van vocalisaties door orang-oetan vrouwtjes. In het hoofdstuk beschrijven we twee casussen. Ten eerste bespreken we het gedrag van Temmy, die specifiek tijdens haar ovulatie sterke interesse toonde in *long calls* van orang-oetan mannen en als reactie op die *long calls* ook zelf een tot nu toe bij experts onbekend geluid produceerde. Daarnaast bespreken we het gedrag van Eloise, die tijdens haar ovulatie een sterke toename in seksuele interesse liet zien richting het mannetje waarmee ze samenleefde. Hoewel dit op zich niet verrassend is, ging het gepaard met de productie van luide vocalisaties, die doen denken aan de *long call* van de mannetjes. Deze casussen laten zien dat vrouwelijke orang-oetans mogelijk een breder vocaal repertoire hebben dan gedacht en dat sommigen van hun vocalisaties mogelijk inzicht kunnen geven in hun seksuele interesse.

In **hoofdstuk 9** reflecteer ik uitgebreid op de resultaten van mijn proefschrift. Met mijn onderzoek heb ik geprobeerd een beter inzicht te krijgen in de rol die cognitieve processen spelen bij partnerkeuze door een vergelijkende benadering te hanteren. Doel van het onderzoek was niet alleen om fundamentele kennis over cognitie en partnerkeuze te verkrijgen, maar ook om cognitieve taken te ontwikkelen die ingezet kunnen worden binnen het Europese fokprogramma voor orang-oetans, om zo individuele partnervoorkeuren te kunnen bepalen. De resultaten in dit proefschrift laten zien dat mensen een robuuste aandachtsvoorkeur hebben voor aantrekkelijke soortgenoten en dat deze voorkeur mogelijk ook voorspellend is voor hun uiteindelijke partnerkeuze. Voor orang-oetans zijn de resultaten minder duidelijk. Hoewel de *eye-tracking* experimenten uit hoofdstuk 8 laten zien dat orang-oetans een aandachtsvoorkeur hebben voor wangplaten, vond ik dit niet terug in de *touchscreen*-experimenten in hoofdstuk 7. Dit roept een hoop vragen op, met name over de manier waarop we cognitie het best kunnen onderzoeken bij dieren. Zo kan het zijn dat er evolutionaire factoren zijn die een taak minder betrouwbaar of valide maken voor specifieke soorten. In het geval van de *touchscreen*-experimenten konden de orang-oetans bijvoorbeeld alleen hun handen gebruiken om het scherm te bedienen, terwijl het voor orang-oetans mogelijk veel natuurlijker is om hun lippen te gebruiken. Daarnaast blijft het een open vraag waarom dieren bepaalde aandachtsvoorkeuren hebben. Keken de orang-oetans meer naar mannen met wangplaten omdat ze die aantrekkelijk vinden of zagen ze die mannen als een bedreiging die ze goed in de gaten moesten houden? Toekomstig onderzoek zou zich daarom kunnen richten op het meten van emoties die de dieren ervaren tijdens cognitieve taken. Dit zou ons wellicht een beter inzicht kunnen geven in de drijfveren van hun gedrag, en daarmee ook dichter bij een betrouwbare methode om partnervoorkeuren te meten door middel van cognitieve experimenten.

Curriculum vitae

Tom Roth was born in 1993 in Amsterdam and graduated from the Ignatius Gymnasium in Amsterdam in 2011. He completed his Bachelor of Science in Biology at Utrecht University *cum laude* (2012-2015). His bachelor thesis investigated how enclosure design influences natural locomotion behaviour in zoo-housed Bornean orang-utans (*Pongo pygmaeus*). Hereafter, he continued with a master in Environmental Biology, specializing in Behavioural Ecology (2016-2018; *cum laude*).

For his first master's research project, supervised by Prof.dr. Liesbeth Sterck (Utrecht University) and Thomas Bionda (Apenheul), Tom used an observational approach to investigate the relation between dyadic aggression, affiliation, and social vigilance in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). For his second master's research project, he performed a field study on aggregation behaviour as a function of fruit availability in Sumatran orang-utans (*Pongo abelii*) in Sikundur Forest (North Sumatra, Indonesia) under supervision of Prof.dr. Serge Wich (Liverpool John Moores University) and Matthew Nowak (Sumatran Orangutan Conservation Programme). For his master's thesis, Tom wrote a research proposal on identifying long-distance methods to test partner preferences in zoo-housed orangutans under supervision of Prof.dr. Mariska Kret (Leiden University).

In 2019, Tom started his PhD at the CoPAN lab, part of the Cognitive Psychology Unit of the Institute of Psychology (Leiden University), in collaboration with Apenheul Primate Park (Apeldoorn). During the project, he was supervised by Prof.dr. Mariska Kret and later also dr. Yena Kim and dr. Juan Olvido Perea-García. During his PhD project he continued the work of dr. Evy van Berlo and Prof.dr. Mariska Kret, who were responsible for installing a touchscreen setup in the enclosure of the Apenheul orang-utans. Tom extended this previous work by also incorporating eye-tracking in the test setup. Furthermore, in collaboration with fellow PhD candidate Tonko Zijlstra and Prof.dr. Mariska Kret, Tom set up two testing facilities (touchscreen & eye-tracking) in the orang-utan enclosure of Ouwehands Zoo.

To collect data with humans and engage the general public in research, Tom ran multiple studies for the general public in Apenheul Primate Park. In addition, he organized a large-scale speed-dating experiment in collaboration with fellow PhD candidate Iliana Samara and Prof.dr. Mariska Kret. Moreover, Tom was involved in teaching in the bachelor Psychology at Leiden University:

he supervised bachelor students during their thesis project and was workgroup teacher for the Consciousness-course.

During the PhD project, Prof.dr. Mariska Kret and Tom initiated a new article type at the Brill-journal *Behaviour*, namely the anecdotal report. He was Guest Editor for anecdotal reports from 2020-2022, and has been Associate Editor at *Behaviour* since the end of 2022.

Since September 2022, Tom works as a lecturer and researcher at the Animal Behaviour & Cognition group (Department of Biology) of Utrecht University.

List of publications

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Roth, T.S., von Wulffen, C., Fox, M., Askew, J., Spierings, M., & Perea-García, J.O. Evidence of female proceptive behaviour and vocalisation during ovulation in two zoo-housed Bornean orang-utan (*Pongo pygmaeus*) females.

In preparation

Roth, T.S., van Berlo, E., Perea-García, J.O., & Kret, M.E. Orang-utans like it cheeky: attentional bias towards flanged males in Bornean orang-utans (*Pongo pygmaeus*).

Roth, T.S., Samara, I., Perea-García, J.O., & Kret, M.E. “I go bananas for you”: Extending sexually selective cognition to nonhuman primates.

Van Berlo, E., Kim, Y., **Roth, T.S.**, & Kret, M.E. Attentional selectivity for emotions: humans and bonobos compared.

Zijlstra, T., Van Berlo, E., **Roth, T.S.**, & Kret, M.E. Exploring attentional biases towards human facial expressions in bonobos (*Pan paniscus*) and humans.