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

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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.

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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.