ORANGUTAN VISION, LOOKING PREFERENCES, AND PASSIVE LOOKING-TIME VERSUS ACTIVE TOUCHSCREEN PARADIGMS

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ABSTRACT

Key aspects of orangutan picture preference, looking paradigms, and vision were assessed in three manuscripts. These studies have important contributions to research on comparative vision and animal picture perception, as well as practical applications for orangutan research. The first manuscript assessed visual preferences for pictures of primates. Orangutan looking-time was coded as they watched simultaneous slideshows on two laptop computers. Orangutans preferred photographs of unfamiliar orangutans over unfamiliar humans, and familiar orangutans over unfamiliar orangutans. When comparing familiar orangutans, they preferred adults over infants, and males over females. These preferences were then compared to preferences reported across primates which show variable results, likely due to complex social factors and context. A second manuscript assessed passive looking-time and active touchscreen paradigms. Passive and active paradigms can produce discrepant results, and the validity of these paradigms had not been empirically assessed in animals. Three methods were compared: looking-time at slideshows on two laptops, a touchscreen that displayed pictures when touched, and simply holding up pairs of printed images. All three methods detected the expected preference for pictures of animals over non-animals. This can be considered evidence of the reliability of these paradigms, equivalence of passive and active methods, and support for continued use of looking-time and touchscreens in orangutan research. The final manuscript assessed the contrast sensitivity function (CSF). Orangutans were trained to select vertical or horizontal lines, and then the CSF threshold was estimated by increasing the spatial frequency and decreasing the contrast of the stimuli. Orangutan CSF was similar in shape and position on the frequency scale to those of humans and macaques, but overall sensitivity was lower. We propose that this was due to testing conditions and low motivation. Across these three manuscripts orangutans demonstrated overall vision and

looking behaviour that was similar to humans, however with high variability likely due to competing interests, low motivation, and individual differences.

DEDICATION

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CHAPTER 1

GENERAL INTRODUCTION

Do orangutans see images as we do?

Look into the eyes of an orangutan, and the orangutan looks back, with eye contact and an attentive gaze. Casual human observers often cite this as evidence of orangutan intelligence and similarity to humans. The similarities between humans and orangutans are indeed well-documented: orangutans are one of our closest relatives in terms of evolutionary history, and they have shown complex cognitive abilities in experiments and field studies. For example, orangutans have demonstrated metacognition (Marsh & MacDonald, 2012), categorization (Marsh & MacDonald, 2008), intentional communication (Bard, 1992), gestural communication including pantomime (Russon, 2018), tool use (Fox, van Schaik, Sitompul, & Wright, 2004), and mathematical abilities such as magnitude and ordination (Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001). However, despite these similarities, it is important that we assess what orangutans see when they gaze back at us: photos have been extensively used in orangutan research and captive life, yet there has been little to no assessment of orangutan vision and perception. In the following research I examined several aspects of what orangutans “see”, beginning with bias in looking at categories of images, including orangutans versus humans, familiar versus unfamiliar orangutans, and age/sex comparisons. The next study assessed orangutan responses to different modalities of displaying images including passively watching slideshows and printed photos, and actively engaging a touchscreen. A final study measured the contrast sensitivity function (CSF), which assesses ability to detect differences in luminance across a range of spatial frequencies. This provides a measure of basic vision, indicating orangutan ability to see fine detail and differences in contrast.

Researchers and caregivers have assumed that orangutans' colour vision, acuity, CSF, motion and depth perception are similar or identical to humans', but these assumptions require verification. Important steps are to measure both basic vision and behaviour relating to perception of more complex stimuli. Research assessing which images orangutans look at spontaneously without food reinforcement informs us about their inner lives, for example, do they differentiate images of objects or familiar individuals? Empirical measurement of these most basic aspects of perception have practical and theoretical applications for research and care of orangutans. By studying how well orangutans see and what they look at, we have the opportunity to improve our understanding of what underpins their gaze, for a deeper understanding of orangutan perception and minds.

Dissertation outline

This dissertation contains three manuscripts (Chapters 2-4), as well as introductory and concluding chapters. Chapter 1 introduces the dissertation, provides information on the natural history of orangutans, and outlines the importance of the project for comparative cognition and perception and for orangutan researchers and caregivers. Chapter 2 is a published manuscript (Adams & MacDonald, 2018) consisting of a series of studies assessing spontaneous visual preferences in orangutans. The chapter begins by discussing the concept of preference, followed by a review of the advantages of spontaneous methodologies and the "preferential looking" paradigm (using untrained looking behaviour to measure cognition). Reports of nonhuman preferences are included such as preference for animals, faces, familiarity, and age/sex characteristics. The second part of Chapter 2 comprises three studies comparing preference for different categories of photos, as measured by looking time at photos displayed simultaneously on two laptop computers. The three studies measured preference for images of (1) orangutans

versus humans, (2) familiar versus unfamiliar individuals, and (3) comparing all members of the orangutan social group according to age/sex categories.

Chapter 3 is a second manuscript (Adams & MacDonald, *submitted*) assessing preference methodology. Passive looking-time and active touchscreen paradigms are evaluated. The chapter opens with reports of visual preference research in nonhuman primates (henceforth 'primates') and their intrinsic interest in pictures. Passive versus active methods are then discussed, in particular the traditional looking-time paradigm in comparison to the increasingly popular touchscreen. In the second part of Chapter 3, three studies assess orangutans' spontaneous preference for photos of animals versus non-animal photos, using (1) passive looking-time at simultaneous photo slideshows on two laptop computers, (2) an active subject-controlled touchscreen that displays images when touched, and (3) a simple method of simultaneously presenting two printed photos. The efficacy of these three methods is compared and suitability for future research will be analyzed.

Chapter 4 is also a published manuscript (Adams, Wilkinson, & MacDonald, 2017) that assesses the visual abilities of orangutans with an estimate of the orangutan CSF. It begins with a review of vision in humans and primates, methods of assessing vision in primates and human infants, and reports of the CSF in primates. Ecological factors that may relate to vision in orangutans are described, including niche, and selection pressures on vision (such as arboreal travel and diet). Then, the qualities of the orangutan eye and brain, and a rationale for assessing orangutan vision are described. The second part of Chapter 4 is an empirical assessment of the CSF of orangutans in which orangutans were trained to select horizontal or vertical lines, and then the spatial frequency and contrast of these lines was decreased until a discrimination threshold could be estimated.

Finally, Chapter 5 discusses research findings, limitations, any potential influences of the prior and concurrent research or inter-test effects, and future research directions. The three manuscripts are presented in approximate order of data collection; see **Appendix A** for the research timeline as well as prior and concurrent research with these orangutans. Data were collected for Study 1 of Chapter 3, then Study 1, 2, and 3 of Chapter 2. Two years later data for Study 2 and 3 of Chapter 3 were collected. Finally, after another two years, data for Chapter 4 were collected.

Ecological factors relevant to orangutan perception

Orangutans are primates of the family Hominidae, commonly known as great apes. They were originally classified as a single species. However, three distinct species of orangutans are now identified: Sumatran orangutans (*Pongo abelii*) the subjects of this study, Bornean orangutans (*Pongo pygmaeus*) (Xu & Arnason, 1996) and Tapanuli orangutans (*Pongo tapanuliensis*) (Nater et al., 2017). Factors that may influence the vision and looking behaviour of orangutans are their habitat, ecological niche, and social demands. They are diurnal and predominantly arboreal (Schmitt, 2010; Thorpe & Crompton, 2009), living in tropical rainforests, primarily in low level areas such as peat swamps and lowland dipterocarp forests (Husson et al., 2009; Rijksen & Meijaard 1999). Their major obstacles to survival are habitat loss, forest fires, and times of low fruit availability (Husson et al., 2009; Morrogh-Bernard et al., 2009). Orangutans do not face much predation other than parasites: Sumatran tigers can be avoided by remaining in trees, although younger individuals are vulnerable to snakes, crocodiles, and clouded leopards (Foitová, Huffman, Wisnu, & Olsansky, 2009; Rijksen, 1978; van Noordwijk, 2009). A major selective pressure on orangutan cognition is the necessity of finding and accessing difficult and embedded foods during times of scarcity (Morrogh-Bernard et al.,

2009; Russon, 2006). In sum, the ecological factors that may be most relevant to orangutan vision and looking behaviour are the demands of arboreal travel and foraging, as orangutans must assess branch supports and locate food sources in the relatively low light conditions of the forest canopy (Morrogh-Bernard et al., 2009; Thorpe & Crompton, 2009).

Key developmental and social characteristics of orangutans are extremely prolonged development (Wich et al., 2009; Wich et al., 2004) and social organization based on female kin clusters and fission-fusion dispersed sociality resulting in loose communities (Mitra Setia, Delgado, Utami Atmoko, Singleton, & van Schaik, 2009; Singleton & van Schaik, 2002; Wich, Geurts, Mitra Setia, & Utami-Atmoko, 2006). Sumatran orangutans begin to acquire the majority of their own food, and transport themselves independently, around 4-6 years of age; however, they remain near their mother until 8-10 years of age (van Noordwijk et al., 2018; van Noordwijk, 2009). Orangutans' prolonged development may influence visual preferences. For example, adult females' preference for faces of infant or young orangutans might be found, as was the case in Japanese macaques (*Macaca fuscata*) and Campbell's monkeys (*Cercopithecus campbelli*), which Sato, Koda, Lemasson, Nagumo, and Masataka (2012) argued was evidence for evolved preference for "cute" infants. Orangutan social organization differs from the large groups typical of chimpanzees and macaques, so perhaps orangutans will display different preferences than have been reported in other primates. In particular, the dispersed sociality could be relevant to familiarity preferences.

Justification: Why study orangutan perception?

Comparisons across species also provide psychologists with alternate models to study the components and mechanisms of psychological processes, including perception and cognition. As our closest living relatives, the great apes provide a valuable source of comparison to humans

with regards to perceptual and cognitive abilities. Orangutans are estimated to share a common ancestor with humans 14 million years ago, earlier than chimpanzee and human divergence (6 million years ago), but still considered close in terms of evolution and taxonomy (Goodman et al., 1998). Orangutans and chimpanzees also display similar cognitive abilities (Leavens, Bard & Hopkins, 2017; Russon et al., 2009). The majority of nonhuman great ape cognitive research has been conducted with chimpanzees, so orangutans offer a valuable alternate perspective with an earlier timeline and geographic isolation in Asia. In assessing hominid phylogeny and ancestry, we can compare across great apes, as well as across prominent taxonomic divides: for instance, monkeys versus apes, and old-world primates of Africa and Asia versus new-world primates of Central and South America. We can estimate the emergence of a given ability through continuity and discontinuity across phylogeny, although there is an ever-present possibility of convergent evolution as is typically recognized between new world *Cebus* monkeys and the great apes (Reader, Hager, & Laland, 2011).

The International Union for Conservation of Nature (IUCN) Red List classifies all three species of orangutans as critically endangered (*Bornean* Ancrenaz, et al., 2016; *Sumatran* Singleton, Wich, Nowak, Usher, & Utami-Atmoko, 2017; *Tapanuli* Nowak, Rianti, Wich, Meijaard, & Fredriksson, 2017). Because of this, it is essential to learn as much as possible about orangutans while the opportunity is available (Preuss, 2010), for knowledge of our close relatives, and for practical reasons such as preserving the species and improving captive care.

The following studies of visual preferences can enrich our understanding of primate picture perception. Despite extensive use of pictures in primate research, there remains disagreement on the nature of primate picture perception, and the abilities and cognitive processes demonstrated when a primate is successful in an experimental task with pictures

(Bovet & Vauclair, 2000; Fagot, Martin-Malivel, & Dépy 2000; Fagot, Thompson, & Parron, 2010). Early research even questioned whether primates could perceive pictures at all, or if they only perceived simpler elements such as patches of colour (Aust & Huber, 2006; Spetch & Friedman, 2006; Winner & Ettlinger, 1979). Further, primates may respond to pictures according to simple cognitive mechanisms such as operant conditioning. If an image is perceived, we must assess if it is interpreted as a real object or as a referent. For example, Parron, Call and Fagot (2008) found that picture-naïve baboons (*Papio anubis*) preferred a real banana slice over a photo of a banana slice. However, in the absence of a real banana slice, they selected a photo of a banana slice over a photo of a pebble and some ate the photo. The baboons potentially did not interpret the photo as referent but rather as a poor exemplar of a banana (Parron et al., 2008). Similar research was conducted with Sumatran orangutans (Reeve, 2012) and reported mixed results. Some individuals may have perceived photographs as representations, while others may have perceived photographs as a series of unrelated perceptual features, and others may have confused pictures as real objects. Spontaneous behavioural responses in picture-naïve individuals are of particular interest. For example, if a picture-naïve subject responds fearfully to a picture of a predator, or approaches images of food, then this is evidence of image perception (for a review see: Bovet & Vauclair, 2000; Fagot et al., 2000). Evidence suggests human infants do not need to learn to perceive images, but do need to learn that pictures are referents (DeLoache, Pierroutsakos, & Uttal, 2003; Preissler & Bloom, 2007). If we find that orangutans have spontaneous visual preference for certain pictures, then this is evidence that they are able to distinguish some characteristics of these pictures without learning.

Studying orangutan perception and visual preferences, then, is critical to interpreting research using pictures. It also offers practical benefits to research, because preferences could

confound research design. Murai and collegues (2005) found a young female chimpanzee had an intrinsic preference for stimuli from the mammal category over vehicle or furniture categories, which could have affected the results of their categorization experiment. Tanaka (1997) reported that a chimpanzee selected pictures of food far more often than other stimuli in a matching-to-sample experiment, and that this had the potential to distort results. Assessment of the basic visual limitations of the system is also essential for any research using pictures, to ensure that the critical features of an image are within the visible range of the subject species. If the features of an image are too low contrast or high spatial frequency, then this could impact response to stimuli. The research presented here is essential and an important step to understanding how orangutans perceive, interpret and respond to pictures. Testing orangutan vision and visual tendencies is important to better understand these critically endangered, cognitively complex, close relatives; to better observe their visual world; and, potentially, to better see their inner lives.

Predictions

The orangutans are predicted to show intrinsic interest in looking at pictures, voluntarily participating with all three apparatuses. In Chapter 2 this interest is predicted to vary according to the content of the pictures, with higher interest for certain categories than for others, including orangutans versus humans, familiar versus unfamiliar, and age/sex preferences. Chapter 3 will assess preference methodologies using pictures featuring an animal (human, orangutan, or other animal) in comparison an inanimate picture (object, scenery, homogeneous field). We predict that both active and passive paradigms will detect a preference for animals, but may differ in effect size, participation, and practical considerations. The basic prediction tested in Chapter 4 is

that orangutans will have similar visual abilities to humans and chimpanzees. The CSF of orangutans is predicted to follow a similar curve to that of humans and chimpanzees.

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CHAPTER 2

Adams, L. C., & MacDonald, S. E. (2018). Spontaneous preference for primate photographs in Sumatran orangutans (*Pongo abelii*). *International Journal of Comparative Psychology, 31*, 1-16.

Note. Due to valuable input from my dissertation committee, Chapter 2 differs from the published version. There were changes to the method of statistical analysis, inclusion of further information, as well as edits to word order and clarification of phrases. Analysis was redone using the R statistics package, which allowed us to do a repeated measures ANOVA making subject a factor. This analysis improved on the prior *t-tests* that had used aggregated scores across subjects, and the prior *t-tests* of raw data within each subject. This more appropriate analysis showed the same outcomes, so it did not change the discussion or conclusions of the paper. **Appendix B** was added to give the reader a summary of visual preference research in primates. **Appendix C** was added to provide a sample of the stimuli. The fact that subjects were captive, not wild, was emphasized for this research, and for the studies cited in the literature review. Characterization of the social structure of orangutans was reworded to “dispersed loose communities centered around female kin clusters” with an updated citation. Study 3 was renamed from “Age/Sex Factors and Relationship Models” to “Age/Sex Social Preferences”. The small samples sizes were explained to be the reason for excluding a more detailed analysis of relationships and kin. Details on kin were developed; for example a column indicating the father of each orangutan was added to **Table 2.1**.

Abstract

Spontaneous looking preferences were assessed in six zoo-housed orangutans. Orangutans were presented with two photographs simultaneously on two identical laptop computers. Preference was measured by calculating the relative looking time for photographs from each stimulus category, over three studies. Four orangutans participated in Study 1 and Study 2, and six orangutans participated in Study 3. Overall, these orangutans exhibited moderate interest in looking at photographs. The results of Study 1 showed that orangutans preferred photographs of unfamiliar orangutans over unfamiliar humans. Study 2 results showed that orangutans preferred photographs of familiar orangutans over unfamiliar orangutans. In Study 3, preferences were assessed using photographs of the nine members of the participants' own orangutan social group. Orangutans preferred photographs of adults over infants, and males over females. Similar studies have reported varied preferences, and we propose that variation is a result of complex demographic and social factors.

Spontaneous Preference for Primate Photographs in Sumatran Orangutans (*Pongo abelii*)

Nonhuman primates exhibit intrinsic interest in pictures, and gaze at some pictures longer than others, a behaviour that can provide insight into cognition and perception (See **Appendix B** for an overview of visual preference research in primates). Typically, animal cognition research employs designs based on trained behaviours or naturalistic observation. Recording a subject's spontaneous responses to stimuli is an alternative option that involves no prior training and no extrinsic reinforcement, and can occur in a more controlled environment. This paradigm has been used successfully to assess preference for certain categories of pictures in chimpanzees (*Pan troglodytes*, Fujita & Matsuzawa, 1986), rhesus macaques (*Macaca mulatta*, Lacreuse, Martin-Malivel, Lange, & Herndon, 2007), and Bornean orangutans (*Pongo pygmaeus*, Hanazuka, Kurotori, Shimizu, & Midorikawa, 2012; Hanazuka, Shimahara, Tokuda, & Midorikawa, 2013). These results can be compared to experiments using training and food rewards that have shown categorization in great apes (*Sumatran orangutans*, Vonk & MacDonald, 2004; *chimpanzees*, Brown & Boysen, 2000; Tanaka, 2001). Similar outcomes across rewarded and spontaneous methodologies reinforce findings, and show that categorization is a cognitive ability that exists independent of training.

The preferential looking paradigm is a method in which the researcher presents multiple stimuli and measures looking time to assess untrained and unrewarded response behaviour (Winters, Dubuc, & Higham, 2015). Preferential looking methods were initially developed to assess visual perception in human infants and animals (Fantz, 1965; Teller, Morse, Borton, & Regal, 1974). Looking time is used to operationalize preference, by comparing the duration and frequency of looking at different stimuli. The term *preference* is used as an indication of interest or attention and is not synonymous with *liking* in this context. The subject may look at a picture

because it is appealing, or because the picture is frightening, or to seek information (Bovet & Vauclair, 2000; Humphrey, 1972; Humphrey & Keeble, 1974). The preferential looking paradigm removes the confounding variable of training effects: when a subject is conditioned to respond to a characteristic of the target stimuli rather than the quality that the researchers are intending to study (Cacchione & Krist, 2004; D'Amato & Van Sant, 1988). Knowing about spontaneous preferences is also important as a basic starting point that takes into account any *a priori* biases that subjects may exhibit to some stimuli over others.

Researchers have consistently found that captive primates show spontaneous preference for pictures of animals. Humphrey (1972) reported that rhesus macaques preferred pictures of animate rather than inanimate objects, while Hanazuka and colleagues (2012) reported that a Bornean orangutan preferred pictures of mammals with four legs over pictures of inanimate objects. A chimpanzee preferred pictures with humans over pictures without humans (Fujita & Matsuzawa, 1986). Chimpanzees preferred video clips of daily activities of chimpanzees or humans rather than a blank screen (Bloomsmith & Lambeth, 2000). Breaux, Watson, and Fontenot (2012) found chimpanzees preferred pictures of chimpanzee body parts over objects. Preference for pictures of faces has been demonstrated across primate species (Parr, 2011) including capuchins, squirrel monkeys (*Saimiri sciureus*, Anderson, Kuwahata, Kuroshima, Leighty, & Fujita, 2005), a gibbon (*Hylobates agilis*, Myowa-Yamakoshi & Tomonaga, 2001), chimpanzees (Kano & Tomonaga, 2009), and human infants (Turati, Valenza, Leo, & Simion, 2005). Face preference has clear adaptive advantages for primate infants due to prolonged maternal dependency and for primates more broadly due to their complex social behaviour.

When viewing pictures of their own species, nonhuman primates have shown preferences for particular age/sex characteristics. Japanese macaques (*Macaca fuscata*) and Campbell's

monkeys (*Cercopithecus campbelli*) showed spontaneous preference for pictures of infants over adults, which the authors argued was evidence of Konrad Lorenz's theory of hardwired attraction to infant-like "cuteness" characteristics (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012). Preference for pictures of infants was also reported in rhesus macaques (Gerald, Waitt, & Maestripieri, 2006), and stumptailed macaques (*Macaca arctoides*, Demaria & Thierry, 1988). Preferences for different stimulus characteristics also vary across participant demographics. Waitt, Maestripieri, and Gerald (2007) found young nulliparous female rhesus macaques looked at pictures of infants longer than did older multiparous females, a finding consistent with juvenile female interest in allocare. Lacreuse and colleagues (2007) reported that female rhesus macaques in their pre-ovulatory cycle preferred pictures of male over female rhesus macaques. This difference was not seen when subjects were in other stages of the ovulatory cycle, and macaques did not exhibit preferences when presented with photos of male and female humans or chimpanzees at any time during their cycle.

Own-species preference has been found in other nonhuman primates and would be predicted by evolutionary theories of other-species avoidance (Demaria & Thierry, 1988; Fujita & Watanabe, 1995; Parr, 2011). Fujita and Watanabe (1995) found four out of five species of macaques preferred pictures of their own species over other macaque species (*Macaca nigra, M. brunnescens, M. hecki, M. tonkeana,* and *M. maurus*), and the one species that did not show own-species preference was an isolated island species (*Macaca brunnescens*). Further evidence of hardwired own-species preference was demonstrated when rhesus macaques preferred pictures of their own-species despite being raised with individuals from another macaque species (Fujita, 1993). However, the same study found that Japanese macaques did not have preference for pictures of their own-species when young; it developed in adulthood and was mediated by

experience (Fujita, 1993). Thus own-species preference may vary across species according to selection pressures and experiential social factors.

An exception to own-species preference is sometimes seen in comparisons of own-species versus humans. Studies of captive chimpanzees have varied results in comparisons of humans and chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). Bloomsmith and Lambeth (2000) did not find a significant difference in captive chimpanzee preference for video of humans or chimpanzees. Tanaka (2003) found chimpanzees preferred pictures of humans over chimpanzees, and a follow-up study (Tanaka, 2007) suggested that preference for pictures of humans was a result of social exposure to humans. Eight adult chimpanzees with high human exposure preferred pictures of humans, whereas three young chimpanzees with less human exposure had no preference or preferred pictures of chimpanzees (Tanaka, 2007). This variability demonstrates that preference must be assessed in multiple situations and contexts across species, for example in the case of Tanaka (2007) chimpanzee preference may reflect conditions of captivity. Study 1 assessed preference for orangutans versus humans because species preference has not been reported in orangutans, and to add to the chimpanzee findings.

Research on spontaneous, unrewarded preference has found some evidence of preference for pictures of familiar individuals over unfamiliar individuals across nonhuman primates, however, results vary. A young human-raised gibbon showed preference for a photograph of its caregiver over a photograph of a human stranger (Myowa-Yamakoshi & Tomonaga, 2001). Chimpanzees showed developmental differences in tracking a picture of their mother over a picture of a comparison chimpanzee. Subjects only preferred a picture of their mother between 4-8 weeks of age; younger (1-4 weeks) and older (8-18 weeks) showed no significant preference, and they also showed no preference for familiar human faces (Myowa-Yamakoshi, Yamaguchi,

Tomonaga, Tanaka, & Matsuzawa, 2005). Analysis of neural activity of a conscious chimpanzee showed different event-related brain potentials when viewing pictures of familiar versus unfamiliar chimpanzees, but not familiar versus unfamiliar humans (Fukushima et al., 2013). Hanazuka and colleagues (2013) found an interesting pattern in an investigation of adult Bornean orangutan familiarity preference: individuals preferred pictures of completely unfamiliar orangutans over current familiar orangutans, but they preferred orangutans familiar from 10 years ago over completely unfamiliar individuals. However, comparisons could not be balanced for sex across current and former categories due to group constraints: three of four familiar orangutans were male but all three former acquaintances were female. So due to confounds of sex and familiarity, it is unclear whether the orangutans preferred unfamiliar individuals or avoided current males. Study 2 compared familiar and unfamiliar orangutans, omitting images of adult males at the request of the zoo. This could assess familiarity without causing arousal due to images of adult males, and contribute a few more subjects to the limited sample sizes characteristic of great ape research.

As discussed above, preference can be influenced by the demographic characteristics of both the stimuli and the participant (Demaria & Thierry, 1988; Gerald et al., 2006; Lacreuse et al., 2007; Sato et al, 2012; Waitt et al., 2007). It is useful to compare these preferences across taxa and species characteristics. For example, group-living and solitary primates may show different preferences, or the very prolonged maternal dependency of orangutans could be associated with an even more pronounced infant preference. For this reason, Study 3 assessed preference across pairs of all members of the orangutan social group to evaluate age/sex preferences and to account for complex demographic and relationship factors which may have been overlooked in previous studies (e.g., using the participant’s mother as a stimulus).

This study assessed spontaneous visual preferences in zoo-housed Sumatran orangutans. Orangutans provide a valuable comparison to humans, of particular interest due to our close phylogenetic relationship, sharing a common ancestor with humans ~14 million years ago (Goodman et al., 1998). Orangutans are an interesting species in which to investigate sociality and face perception because they live in dispersed loose communities centred around female kin clusters (Mitra Setia et al., 2009; Singleton & van Schaik, 2002). Caregivers of captive orangutans often display pictures or videos, and zoos have recently incorporated touchscreens and iPads into orangutan enrichment programs (Boostrom, 2013; Perdue, Clay, Gaalema, Maple, & Stoinski, 2012), so the study of orangutan preference also has practical applications. Reports of orangutan preferences can aid in research design, to help avoid stimulus confounds due to *a priori* preferences. Taken together, spontaneous preference data can shed considerable light on nonhuman primate social behaviour, and how these species view their world.

Study 1: Orangutans versus Humans

The preferential looking paradigm was used to measure spontaneous preference for photographs of orangutans in comparison to photographs of humans. Two identical laptop computers presented simultaneous slideshows, one featuring photographs of unfamiliar orangutans and the other featuring photographs of unfamiliar humans. Orangutan looking behaviour at each of the slideshows was coded as a measure of preference. We predicted that the orangutans would look preferentially at photographs of orangutans rather than at photographs of humans.

Method

Subjects

Eight orangutans at Toronto Zoo were available to participate but sample sizes fluctuated across Study 1, 2, and 3 due to circumstances and orangutan motivation. The orangutans

included an adolescent female (Jahe), an adult male (Molek), and three mother-infant dyads: Puppe and Budi, Ramai and Jingga, Sekali and Kembali. Dinding, an older adult male, died before formal data collection began, but his data were included in the pilot phase. Age/sex and social characteristics are shown in **Table 2.1**. We collected data in the off-exhibit enclosures and play areas, and no changes were made to the orangutans' schedule or diet. In order to be included in the study the orangutans were required to remain in the front two meters of the enclosure and look at each screen at least once during a set of stimuli. The two youngest orangutans, Jingga and Kembali, were often distracted and so did not meet these criteria during Study 1 and 2. Data from two adult female orangutans were excluded from all three studies. One (Puppe) had misaligned eyes so it was difficult to determine the direction of her gaze, and the other (Sekali) was not motivated to participate. We designed the research to concurrently serve as enrichment for the orangutans. Procedures complied with ethical guidelines of the Toronto Zoo and York University.

Table 2.1

Age/sex Characteristics and Social Relationships of the Subject Orangutans

Subject	Sex	Age (*yrs*)	Experimental history	Rearing	Mother; Father
Infants and nulliparous adolescent female					
Jingga	F	1.5	Naïve	Captive born, orangutan reared	Ramai; Molek
Kembali	M	2	Naïve	Captive born, orangutan reared	Sekali; Molek
Budi	M	2.5	Naïve	Captive born, orangutan reared	Puppe; Molek
Jahe	F	11	Cognitive studies	Captive born, orangutan reared	Puppe; Molek
Adult females					
Sekali	F	16	Cognitive studies	Human and orangutan reared (adoptive mother Ramai)	Abigail; Dinding
Ramai	F	23	Cognitive studies	Captive born, orangutan reared	Chantek (Abigail; Mias); Dinding
Puppe	F	Estimated 41	Cognitive studies	Wild caught	Wild
Adult males					
Molek	M	30	Cognitive studies	Captive born, laboratory	Other zoo
Dinding	M	Estimated 50	Cognitive studies	Wild caught	Wild

Note. Age is age at time of study. Jahe, Sekali, Ramai, Puppe, Molek, and Dinding had all participated in several cognitive studies, for example rewarded touchscreen categorization experiments (Vonk & MacDonald, 2004; Marsh & MacDonald, 2008).

Materials

Apparatus. Photographs were presented on two identical Apple PowerBook G4 laptop computers with 30.5 cm screens using Microsoft® Office PowerPoint. The laptops were placed at a height of 28 cm from the ground, 30-60 cm apart, and 50-100 cm from the orangutans. Distances varied to optimize viewing angles for infant, adult female, and adult male subjects. Eye orientation was recorded by a video camera on a tripod located between the two screens. Two slideshows, each displaying photographs for five seconds, were presented simultaneously to

the individual subject. Preference was calculated as the mean time (in s) that the orangutan spent looking at the target photograph compared to the comparison screen.

Stimuli. The stimuli were color photographs resized to fill at least 50% of the screen. We obtained the stimuli from photographs taken by the research team, zoo staff and volunteers, and through internet searches. All stimuli in Study 1 featured unfamiliar individuals. Photographs of human infants and human adult females were compared to equal numbers of photographs of orangutan infants and orangutan adult females. At the request of the zookeepers, photographs of unknown adult male orangutans were excluded to minimize stress on the orangutans, particularly the adult male subject. Correspondingly, we omitted photographs of adult human males. Photographs were balanced so that both orangutan and human stimuli included some images that featured faces, and others that included the full body. We roughly matched body position and other features of the images, such as eye gaze directed at the camera, and the presence of other colourful objects in the background. See **Appendix C** for a sample of the stimuli used. The two simultaneous slideshows each contained 20 photographs resulting in a total of 40 photographs for each testing session. The 20 comparisons were separated into two units of 10 comparisons, so that a stimulus category displayed sequentially for 10 slides on one screen. This was done to mitigate the effect of any one photograph. We signaled the change of unit, and therefore changing content of slides, with a loud chime sound, two blank slides, and a brief pause. Presentation order was counterbalanced across trials, subjects, and left and right screen locations.

Measures. The data were coded from videotape by two trained coders who were blind to the content and order of the slideshows using TakLin SubTrak software (Takach & Lindtvedt, 2005). Interrater reliability had an overall Cohen's kappa of 0.83. Eye orientation was coded at 0.1s intervals, which was comparable to coding video frame-by-frame. From these data, the total

duration of looking behaviour and the mean looking time were calculated for each stimulus category. To build on this quantitative data, a second round of coding applied a qualitative code of preferred side for each unit. The coders watched the videotape in real-time and chose a preferred side using a forced-choice judgement of preference (Teller et al., 1974) taking into account behavioural indicators of preference, such as leaning closer to one screen, body orientation, double-takes, facial expressions and vocalizations (Rijksen, 1978), as well as perceived looking behaviour. Both quantitative and qualitative methods of coding were done with the coder blind to the content of the slideshows and blind to prior codes.

Procedure. We conducted the trials simultaneously for mother-infant pairs, and separately for individuals housed in single enclosures. We called the orangutans' names to alert them that a slideshow was about to begin, and began the testing session when an orangutan was within the front two meters of their enclosure. We did not provide any incentives or food rewards. We presented the slideshow until completion, but ended the slideshow early if the orangutan departed from the front two meters of the enclosure, or exhibited more than a few instances of agitation behaviour (e.g., facial expressions and vocalizations). For individuals who did not complete the slideshow up to two additional attempts were provided. Data resulting from duplicated views were removed, so that only the first instance was used for analysis. Researchers remained hidden behind the apparatus to avoid cueing the orangutans and were blind to the stimuli and slideshow order.

The study was designed to measure spontaneous behaviour, so a period of training was neither necessary nor desirable. Two practice slideshows were done to allow for calibration of the apparatus, initial technical difficulties, and orangutan habituation to the researchers and apparatus. Results from these two sessions were not included in the data analysis. Statistics were

performed using a repeated measures ANOVA in R version 3.5.1 (R Core Team, 2018), RStudio (RStudio Team, 2016), and lme4 (Bates, Maechler, Bolker, & Walker, 2015).

Results and Discussion

Four orangutans met the inclusion criteria. These orangutans looked at the screens on average 59% of the time (range: 27% - 81%), as shown in **Table 2.2**. We predicted that the orangutans would prefer photographs of orangutans over photographs of humans. A repeated measures ANOVA was conducted with subject as a factor to account for multiple data points from the four available orangutans. A linear mixed effects analysis was used to assess the effect of stimulus (pictures of orangutans or humans) on duration, with subjects as a random effect. P-values presented are a comparison of likelihood ratio of the full model in comparison to a model without stimulus as an effect. As shown in **Figure 2.1**, average looking-time was significantly longer for photos of orangutans, (M = 1.36, SD = 0.38), than photographs of humans, (M = 0.87, SD = 0.36), $F(1,3) = 12.40$, $p = 0.00049$ (**Table 2.2**). The qualitative data codes matched all the quantitative measures of preference.

Table 2.2

Participation and Looking Time (seconds) at Photographs of Orangutans Versus Humans

Subject	Time looking	Orangutan *M (SD)*	Human *M (SD)*	Qualitative preference
Budi	50.3%	1.20 (1.43)	0.68 (0.48)	Orangutan
Jahe	80.7%	1.83 (1.26)	1.28 (0.82)	Orangutan
Ramai	27.0%	0.93 (1.01)	0.49 (0.45)	Orangutan
Molek	70.7%	1.48 (1.40)	1.05 (1.29)	Orangutan

Note. For the remaining analysis orangutan subjects are listed in order by age-sex group: infants, adolescent, adult females, adult male. Data only include times when the orangutans were within the first two meters of the enclosure, videotape was clear and unobstructed, photographs were present on both screens, and eyes were open (blinks removed).

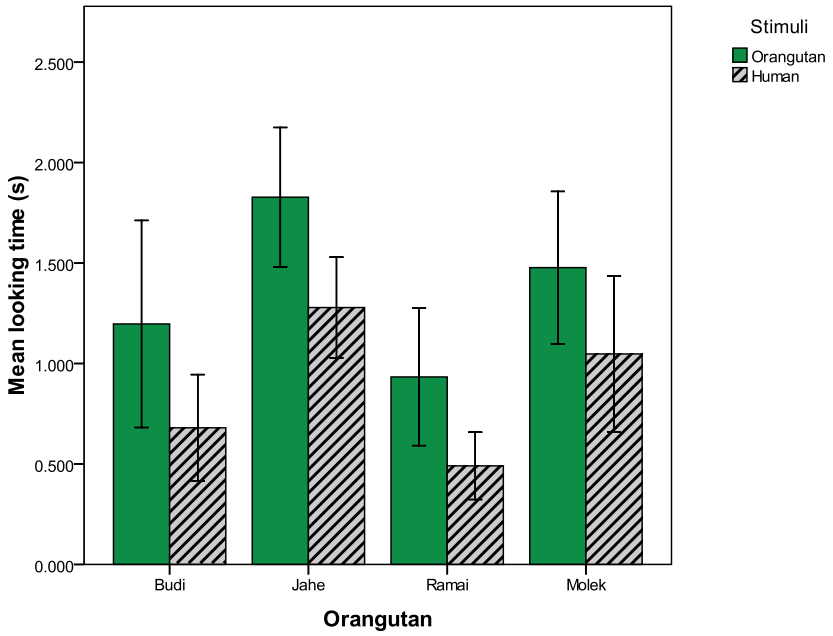

Figure 2.1. Mean time looking at photographs of orangutans and photographs of humans (error bars indicate 95% confidence intervals).

In this study, orangutans clearly preferred viewing photographs of orangutans over photographs of humans. This is consistent with own-species preference in macaques (Demaria & Thierry, 1988; Fujita & Watanabe, 1995; Parr, 2011), however it differs from studies of adult captive chimpanzees that found preference for images of humans over chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). This finding may differ from the chimpanzee studies due to species differences, or due to different conditions of captivity such as the nature of the chimpanzees' relationships to human caregivers. The Toronto Zoo setting places priority on maintaining social bonds among orangutans rather than with humans.

Study 2: Familiar versus Unfamiliar Orangutans

Method

Study 2 used the same method, apparatus, subjects, and procedure as Study 1 with the exception of the content of the stimuli. The stimuli featured photographs of familiar orangutans and unfamiliar orangutans, with the prediction that orangutans would prefer familiar orangutans. Stimuli featured both faces and full bodies, for a sample see **Appendix C**. As with Study 1, each slideshow was composed of two units of 10 comparisons, for a total of 40 photographs shown, and we did not use photos of adult males. Photographs compared images of Jahe, an adolescent female member of the group, to one unfamiliar age-matched female orangutan, and photographs of familiar adult females with offspring to matched unfamiliar adult female orangutans with offspring.

Results and Discussion

Preference for familiar versus unfamiliar orangutans was calculated using the same methods as Study 1. The same four orangutans met the inclusion criterion, and average participation rate was 62%, range = 15% -97%, as shown in **Table 2.3**. A repeated measures

ANOVA using a linear mixed effects model found a significant main effect of stimulus on duration. As shown in **Figure 2.2**, average looking-time was significantly longer for photos of familiar orangutans (M = 1.70, SD = 0.99) than unfamiliar orangutans (M = 0.93, SD = 0.58), $F(1,3) = 13.54$, $p = 0.00029$ (**Table 2.3**). As in study 1, qualitative data codes matched quantitative measures of preference.

Table 2.3

Participation and Looking Time (seconds) at Photographs of Familiar Versus Unfamiliar Orangutans

Subject	Time Looking	Familiar *M (SD)*	Unfamiliar *M (SD)*	Qualitative preference
Budi	29.1%	1.41 (1.54)	0.42 (0.26)	Familiar
Jahe	96.9%	3.00 (1.68)	1.51 (1.13)	Familiar
Ramai	15.3%	0.63 (0.50)	0.45 (0.38)	Familiar
Molek	83.7%	1.77 (1.80)	1.34 (1.39)	Familiar

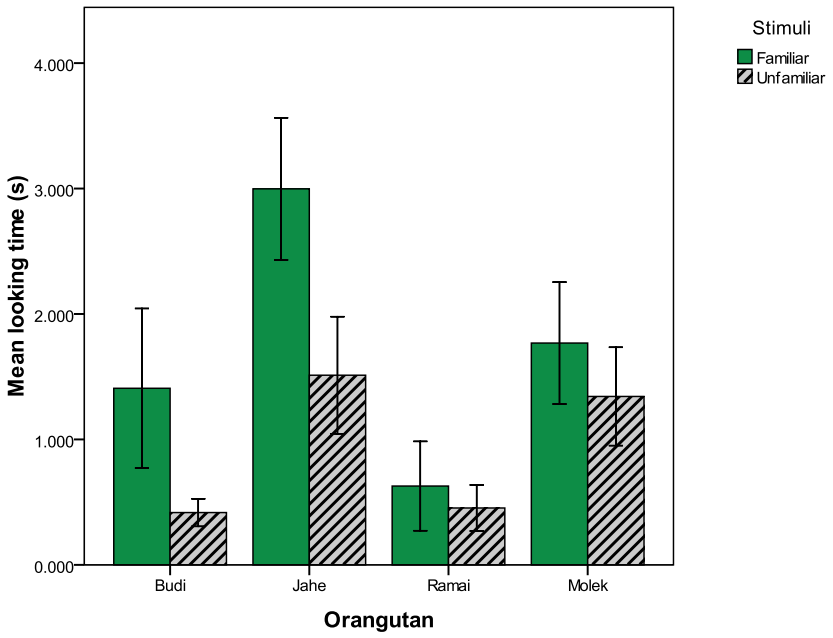

Figure 2.2. Mean time looking at photographs of familiar and unfamiliar orangutans (error bars indicate 95% confidence intervals).

Results showed a moderate preference for photographs of familiar orangutans over unfamiliar orangutans. Prior research using a matching-to-sample paradigm found that orangutans (*Pongo abelii*) could match photographs of familiar conspecifics, although it was unclear if this matching was due to the similarity of the features in the photographs or recognition of familiar individuals (Vonk & Hamilton, 2014). Note that one of our subjects, Molek, had participated in a prior study (Vonk & MacDonald, 2004). This prior experience did not appear to bias Molek as he showed moderate familiarity preference in comparison to the other orangutans in the study. Talbot, Mayo, Stoinski, and Brosnan (2015) also tested orangutan (*Pongo spp.*) matching-to-sample for conspecific faces and found that orangutans performed better with familiar conspecifics. As discussed in the introduction, many nonhuman primates

have shown preference for images of familiar over unfamiliar individuals (Myowa-Yamakoshi & Tomonaga, 2001; Myowa-Yamakoshi, et al., 2005). Our results are not consistent with Hanazuka and colleagues (2013) who found preference for unfamiliar orangutans over current acquaintances. We propose that this difference is due to social, demographic, and relationship factors as discussed below.

Context or social factors are likely relevant to familiar versus unfamiliar preferences, such as species characteristics and grouping patterns, for example solitary versus social, and stable versus fluctuating groups (Parr, 2011). Within species, individual differences and relationships may influence preferences. For example, kin may elicit looking behaviour, and rivals could either elicit avoidance or vigilant looking. Preference research on familiarity is by nature confounded: comparisons pit preference for conspecifics against preference for novelty (Houston-Price & Nakai, 2004; Roder, Bushnell, & Sasseville, 2000). Further, adult orangutans may have conflicting preferences according to mating strategy and reproductive state, if familiar individuals are paired against potential novel mates and competitors. Our familiar versus unfamiliar comparison could have been confounded with a factor such as kin versus non-kin, as some of the familiar stimuli would have been kin for each of the subjects. Unfortunately, with the small sample sizes characteristic of great ape research, it is difficult to determine whether familiarity is the driver of behaviour or whether other and/or additional demographic characteristics, social dynamics, and kinship are responsible. The moderate preference for familiarity in the current study may reflect some of these complex social factors, which were further explored in Study 3.

Study 3: Age/Sex Social Preferences

The method, apparatus, subjects, and procedure for Study 3 were identical to Study 1 and 2, however the content of the stimuli and number of photographs differed. The stimuli were paired-comparisons of photographs of all nine resident orangutans at Toronto Zoo, so participants viewed photos of themselves and each of their close conspecifics. Each slideshow included 10 pairings of orangutan individuals. Each pairing showed five different images of each of the individuals, for a total of 50 slides on each computer. Four testing sessions were required to show all 36 comparisons of individuals. Stimuli depicted the orangutan on a white background, with other parts of the photo removed using Photoshop CS3. See **Appendix C** for a sample of the stimuli.

We predicted orangutans would show different preferences according to the age/sex characteristics of both the subject (subject-orangutan) and the photo stimuli (stimulus-orangutan). We evaluated preference using comparisons of photographs of all of the orangutans at the zoo. The time spent looking at each stimulus-orangutan was calculated. We assessed age/sex classes of stimuli, comparing time looking at infants versus adults, and adult females versus adult males. The adolescent Jahe was excluded from age comparisons because she was at an intermediate age, entering puberty at the time of testing. We had originally planned to assess preference across subjects and relationships. This analysis could not be completed due to the results of the age/sex comparisons, in combination with small sample sizes and confounds as described below.

Results and Discussion

Six orangutans met the inclusion criterion, including the young Jingga and Kembali. All subjects watched at least 30% of the time (M = 48.90%, SD = 19.29, range 31%-83%).

Consistent with Study 1 and 2, Molek and Jahe had the highest participation. As described in Study 1, a repeated measures ANOVA using a linear mixed effects model was used, and there was a significant main effect of stimulus on look duration. Average looking-time was significantly longer for photos of adults (M = 0.64, SD = 0.09) than infants (M = 0.36, SD = 0.09), $F(1,5) = 7.24$, $p = 0.00731$ (**Figure 2.3**). We then compared preferences for all times that a photograph of an adult female was paired against an adult male. Average looking-time was significantly longer for photos of males, (M = 0.64, SD = 0.11), than females (M = 0.37, SD = 0.11), $F(1,5) = 12.06$, $p = 0.00061$ (**Figure 2.4**).

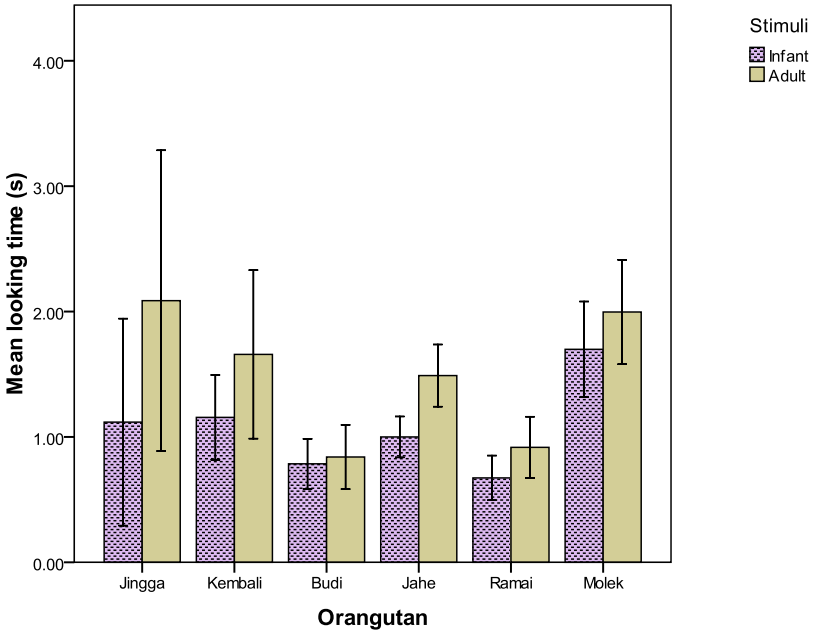

Figure 2.3. Mean time looking at photographs of infants or adults. Calculated using all simultaneous presentations of an infant and an adult (error bars indicate 95% confidence intervals).

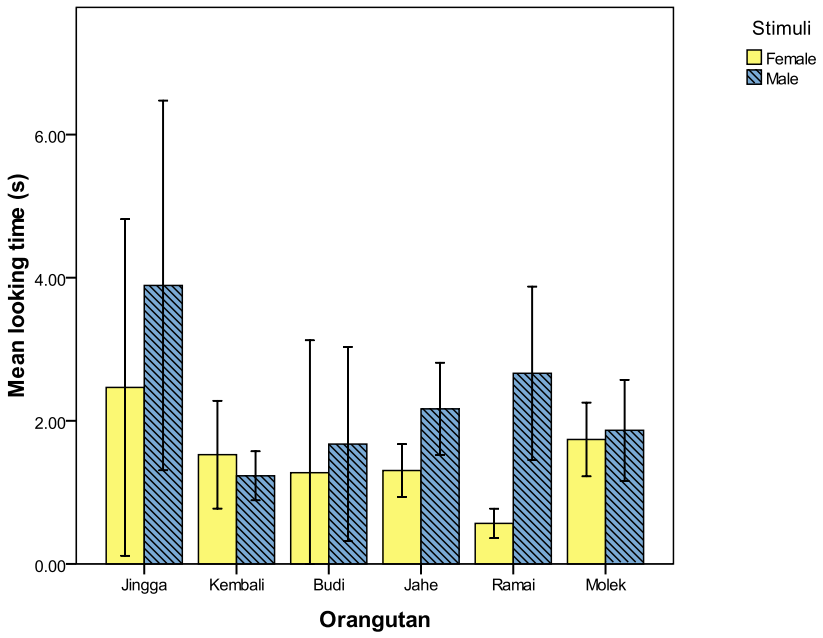

Figure 2.4. Mean time looking at photographs of females and males. Calculated using all simultaneous presentations of a female and a male (error bars indicate 95% confidence intervals).

After the age/sex differences were assessed for the stimulus-orangutans, we planned to assess preference across the age/sex characteristics of the subject-orangutans, kin relationships, as well and across the two matrilineal social groups. However, all subjects showed longer average looking time for adults over infants, and all but one subject preferred males over females. As a result, sex preferences that we would assess across subjects would be limited to interaction effects, for example if females showed a larger preference for males than male preference for males. Sample sizes were too small to conduct this analysis. Further, an analysis of relationships would have been valuable, for example, measuring infant preference for pictures of their own mother over pictures of the other two adult females. However, these subgroups had small and unbalanced samples. Similarly, we had hoped to assess preference across matrilineal

social groups (Puppe, Jahe, Budi, versus Sekali, Ramai, Kembali, Jingga). We opted to not complete this exploratory analysis due to small unbalanced samples, as well as confounds of kinship and housing plus mitigating variables such as aggressive conflicts between the orangutans.

Orangutans spent more time watching the slideshows in Study 3 than the two previous studies. They demonstrated moderate preference for adults over infants, and males over females. Observed orangutan preference for photographs of adults over infants differed from research reporting preference for infants over adults in female rhesus macaques (Gerald et al., 2006), and Japanese macaques and Campbell's monkeys (Sato et al., 2012). Our findings do not support the idea that orangutans have an evolved preference for "cuteness" as suggested by Sato and colleagues (2012), or it may be that interest in adult males outweighed the cuteness effect. Orangutan social patterns differed from those of the above monkey species, so perhaps orangutan preference for adult males instead of infants is a reflection of orangutan dispersed matrilineal kin clusters: adult males are important to attend to and are more novel than females and young. The preference for photographs of adult male over adult female orangutans was also in opposition to macaque research that reported preference for the opposite sex (Lacreuse et al., 2007), and prior observations with these orangutans (Marsh & MacDonald, 2008). The inconsistency with Marsh and MacDonald (2008) rests on the single adult male orangutan available for both studies. In our study Molek had longer looking time at male orangutans, whereas for Marsh and MacDonald (2008) he had a preference for adult females. This highlights the difficulty in assessing demographic preferences in such small groups.

Different findings may reflect species-differences between orangutans and macaques relating to species-typical patterns in dominance and social group organization, or a result of

demographic and social characteristics of these particular individuals. We did not see differences in age preference between female and male subjects. Individual and relationship factors could also explain this discrepancy. Prior social conflict between our adult females could have increased looking time at rivals, obscuring infant preference. Dinding's recent death could have influenced the higher looking time at adult males, however images of Molek were also preferred. Complex social and relationship factors make Study 3—and the results of previously published research—difficult to interpret definitively.

General Discussion and Conclusions

In Study 1 orangutans preferred photographs of their own species over photographs of humans, a result consistent with macaque own-species preference (Fujita & Watanabe, 1995; Parr, 2011) but differing from adult chimpanzee preference for pictures of humans over chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). In Study 2, orangutans showed a moderate preference for familiar over unfamiliar orangutans, in comparison to mixed reports of familiarity preference (Hanazuka et al., 2013; Myowa-Yamakoshi et al., 2005; Myowa-Yamakoshi & Tomonaga, 2001; Parr, 2011). In Study 3, the orangutans preferred photos of adults over infants, which differs from reports of infant preference in other species (Gerald et al., 2006; Sato et al., 2012). Prior research has reported opposite sex preference (Lacreuse et al., 2007; Marsh & MacDonald, 2008), which was consistent with our female preference for photos of males, but not consistent with our male orangutan preferring images of males.

The variability in findings across preference research likely reflects multiple interacting variables including species, social factors, and individual characteristics and experience. Preferences may vary across species, and the species niche such as diet and grouping patterns could select for a bias in attention to certain stimuli. Preferences may also depend on the

situation and conditions of captivity and rearing, including amount and quality of relationships with humans and conspecifics, group dynamics, and housing. Finally, preference may depend on individual differences, temperament, and demographic characteristics of the subject. For example, Fujita and Watanabe (1995) found species preference was less pronounced in female macaques than in males (*Macaca nigra*). Sekali (adult female) was excluded in our study due to low participation rate, however her limited data differed from the other orangutans. This is interesting to note because she had been partially human-reared, potentially supporting the social exposure hypothesis of Tanaka (2007).

Unfortunately, small sample sizes in great ape research make it difficult to account for interactions across age, sex, and relationships of both the individual participating and the individual featured in stimuli. The three adult females were mothers of young offspring, which could be associated with different preferences, for example, increased vigilance to other orangutans to protect offspring. Relationship models would predict preference for some members of the social group over others; for example, mother-infant pairs may prefer pictures of each other, and males or sexually receptive females may prefer pictures of possible mating partners. A supposed preference for females could owe to a preference for pictures of the subject's own mother rather than females per se, a distinction that is hard to assess with small samples. Study 3 was an attempt to account for relationship factors; however, we were unable to assess relationship trends, and this may be too complex a question to assess with the small samples characteristic of captive great ape research. Nulliparous rhesus macaques showed higher infant preference than multiparous female macaques (Waitt et al., 2007). Jahe, our only nulliparous adolescent female, did not show infant preference. In some cases, social interests may cancel each other out: infants elicit looking behaviour, but so do potential sexual partners and

competitors. As discussed in the introduction, preference is not synonymous with liking: individuals may look longer at certain pictures due to fear, attraction, negative associations, or attachment. Preference may be influenced by further factors not measured, such as ovulatory cycle (Lacreuse et al., 2007). The varied research reports of preference likely reflect the complexity of the social factors, relationships, and demographics of captive primates.

The demonstrated preferences provide insight into the perceptual world of orangutans by showing what orangutans look at spontaneously. Our findings cannot identify inner mechanisms; for example, a demonstrated preference for own-species could employ sophisticated cognitive processes or it could be explained by more simple innate mechanisms. However, significant differences in looking time for different categories, such as orangutans versus humans, are, at minimum, evidence that some difference is perceived between these categories. Likewise, preference for either familiar or unfamiliar orangutans, regardless of which is preferred, is indicative of nonhuman primate capacity to recognize familiar individuals from pictures without training. Ability to recognize individuals is likely important to successful group membership in primates given the nature of their sociality, and if a nonhuman primate can recognize a conspecific from a picture using two dimensional visual cues without other indicators, then this can inform our understanding of primate perception. These findings complement the findings of other experimental designs, such as matching-to-sample of familiar and unfamiliar conspecifics (*orangutans*: Talbot et al., 2015; Vonk & Hamilton, 2014; *chimpanzees:* Martin-Malivel & Okada, 2007; Parr, Siebert, & Taubert, 2011), and provides evidence that orangutans do not need training to distinguish these photographic stimuli. Better understanding of picture perception is essential because of the prevalent use of pictures in research. DeLoache, Pierroutsakos, and Uttal (2003) argue overestimating pictorial competence of human infants is a methodological problem,

and that use of pictorial versus real stimuli might explain some controversies in human infant research.

The participation rates of the orangutans varied, showing that this spontaneous looking paradigm is useful with some but not all subjects. The youngest individuals had low participation, instead choosing to engage in high energy active play. Jahe (adolescent female) and Molek (adult male) exhibited high rates of interest, watching the majority of the slideshows on all occasions. Overall the looking preference apparatus functioned as a source of enrichment, however, given the discrepant levels of interest and motivation across individuals and studies, caregivers should first assess individuals' interest before implementing it as an enrichment program (MacDonald & Ritvo, 2016; Ritvo & MacDonald, 2016).

The preferential looking paradigm is useful when there is a large preference effect size. However this method may not be useful to assess subcategories and smaller distinctions. For example, comparisons between high and low interest stimuli (e.g., animal versus non-animal) can be distinguished by looking time. The comparisons in the current research, particularly Study 3, both featured attractive photos making it difficult to detect differential looking at a marginally more attractive category. Difficulty in distinguishing preference with finer grained category differences was demonstrated in chimpanzees: they preferred video of humans and chimpanzees over a blank screen; however, there were no specific content preferences across comparisons of humans versus chimpanzees, or videos of different activities (Bloomsmith & Lambeth, 2000). Breaux and colleagues (2012) found that chimpanzees preferred pictures of chimpanzee body parts over inanimate objects, but did not find the predicted preference for specific characteristics of sexual body parts in comparison to other body parts. Finer grained distinctions may be particularly difficult if there are competing interests; for example, familiarity versus novelty.

Human infant research reports looking preference for familiar stimuli in some cases but there is also an established preference for novelty, depending on stimuli and context (Houston-Price & Nakai, 2004; Roder et al., 2000). These competing preferences must be accounted for in human infant research design. Novelty of stimuli could influence research outcomes, for example, in the case of Breaux and colleagues (2012) chimpanzees did not prefer photos of the predicted pink sexual swellings over photos of (artificially created) green sexual swellings. Perhaps preference for a typical sign of sexual receptivity was obscured by the novelty of the artificial comparison stimuli. The complex patterns of preference in chimpanzees and orangutans (Hanazuka et al., 2013; Tanaka, 2007; Vonk & Vedder, 2013) are not surprising given their close phylogenetic relationship to humans. To our knowledge similar studies have not been conducted with human adults, but we would predict that results may show similar complexity; that is, humans may show conflicting preference for cute infants versus attractive adults.

Although the preferential looking paradigm has limitations, its advantages include removing the risk of training effects and focusing on voluntary behaviour (*for a review of the looking time paradigm see* Winters et al., 2015). Participation in studies using this paradigm is solely motivated by intrinsic interest, so preference research is non-invasive and can concurrently function as enrichment. The paradigm provides a valuable alternative to experiments based on extensive training or to naturalistic observation. Efficiency of this paradigm could be improved with eye-tracking technology, which Kano and Tomonaga (2009) have successfully used with chimpanzees. This avoids time-consuming coding, so we hope that eye-tracker expense and feasibility will improve to allow use with free-moving untrained subjects from a wide range of species in non-laboratory settings.

It is important to document preferences to better understand how a species views their world, to inform cognition research, and to limit confounding variables in research that employs pictures as experimental stimuli. Spontaneous preferences, like those demonstrated here, show that orangutans are able to perceive and distinguish some aspects of photographs without training, which suggests that orangutans may look at photographs as humans do, with varied influence from social relationships, experience, and demographics.

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CHAPTER 3

Adams, L. C., & MacDonald, S. E. (*submitted).* Assessing unrewarded photo preference in orangutans (*Pongo abelii*): Comparison of passive looking-time and active touchscreen methods. Manuscript submitted for publication

Abstract

The use of photographs has become ubiquitous in animal cognition research. In this study, the spontaneous unrewarded photo preferences in eight Sumatran orangutans (*Pongo abelii)* were assessed using three methods, all designed to measure the same quality: preference for images containing animals over images without animals. In Study 1, two computer screens displayed photo slideshows simultaneously and looking-time at photos was recorded. In Study 2, a touchscreen computer allowed subjects to control how long a photo was displayed. For Study 3, the method was to simply hold up pairs of printed photographs. The three methods differed according to level of orangutan interest and participation, and practical considerations. As expected, the results of all three studies showed a preference for photos containing animals rather than photos without animals, which can be considered support for continued use of passive looking-time and active touchscreen methods.

Assessing unrewarded photo preference in orangutans (*Pongo abelii*): Comparison of passive looking-time and active touchscreen methods

Picture stimuli are a popular choice in cognition research with primates to investigate diverse abilities, for example, photos have been used to study orangutan categorization (Marsh & MacDonald, 2008; Vonk & MacDonald, 2004), memory (Swartz, Himmanen, & Shumaker, 2007), spatial strategy (Marsh, Adams, Floyd, & MacDonald, 2012), and preference (Adams & MacDonald, 2018), (for reviews of photo use in animal research see Bovet & Vauclair, 2000; Fagot, Martin-Malivel, & Dépy, 2000; Fagot, Thompson, & Parron, 2010). However, it is unlikely that all primate species perceive pictures as humans do (Bovet & Vauclair, 2000; Fagot, et al., 2010; Parron, Call, & Fagot, 2008). Subjects may behave differently across experimental methods due to different aspects of the apparatus, such as whether the subject is passive (i.e. watching and reacting to stimuli) or active (i.e. touching a touchscreen or pressing a button). Human children have shown different results in passive and active tasks that purportedly test the same ability (Charles & Rivera, 2009; Hood, Cole-Davies, & Dias, 2003; Shinskey & Munakata, 2005), as have rhesus macaques (*Macaca mulatta*) (Santos & Hauser, 2002). The purpose of this study was to evaluate passive and active methods of assessing spontaneous picture preferences of Sumatran orangutans (*Pongo abelii),* in particular, assessing use of looking-time and touchscreen methods.

Visual preference

In picture preference research the operational definition of *preference* is an observed bias to one stimulus rather than another, for example, looking at picture A more than picture B. Preference is not assumed to mean that the stimulus is attractive or pleasing to the subject, only that it elicits more attention than a comparison stimulus. For example, pictures of predators elicit

looking behaviour in many species (Bovet & Vauclair, 2000; Humphrey & Keeble, 1974). Bias toward one set of stimuli is an interesting finding because an *a priori* preference can give insight on cognitive and evolved mechanisms, and because there are practical consequences to stimuli bias in experimental contexts as well as in captive care.

Voluntary viewing of pictures without food rewards is reported in many primate species in captivity including chimpanzees (*Pan troglodytes*) (Fujita & Matsuzawa, 1986); Sumatran orangutans (Adams & MacDonald, 2018); capuchins (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*) (Anderson, Kuwahata, Kuroshima, Leighty, & Fujita, 2005), and several macaque species (*Macaca sp*. Fujita & Watanabe, 1995). For example, Fujita and Matsuzawa (1986) found that a chimpanzee looked at pictures for 1000 trials without reinforcement, and the researchers attributed this behaviour to the "reinforcing nature" (p. 290) of the stimuli. Touchscreens and pictures are popular sources of cognitive enrichment for captive orangutans (Boostrom, 2013; MacDonald & Ritvo, 2016; Perdue, Clay, Gaalema, Maple, & Stoinski, 2012; Webber et al., 2017; Wirman, 2013). Taken together, pictures and other visual stimuli appear to be intrinsically rewarding to at least some primates.

Researchers have reported preference for certain categories of stimuli: a consistent finding across species is preference for pictures featuring animals rather than pictures without animals (*chimpanzees* Fujita & Matsuzawa, 1986; Kano & Tomonaga, 2013; *Bornean orangutans* - *Pongo pygmaeus* Hanazuka, Shimizu, Kurotori, & Midorikawa, 2012; *rhesus macaques* Humphrey, 1972; *gibbon* - *Hylobates agilis* Myowa-Yamakoshi & Tomonaga, 2001). There are multiple candidates for the mechanism of these preferences. Visual attention to key environmental stimuli would have adaptive value; for example, looking to animals is vital in predator and prey contexts, so it would be advantageous for this behaviour to be innate. Japanese

macaques (*Macaca fuscata*) detect images of snakes more quickly than other images even if they have never encountered a snake (Kawai & Koda, 2016). Systematic study of visual preferences across phylogeny may also reveal inter- and intra-species trends. For example, Balling and Falk (1982) found that humans preferred images of savanna over other landscapes and concluded that this could be an innate evolved preference for our ancestral habitat, a claim that could be further assessed by evaluating cross-species preferences for habitat photos.

Looking preference may also involve more complex cognitive mechanisms. For example, humans may attribute their preference for one image over another to aesthetics, personality, experiences, thoughts and beliefs, or mood. Shettleworth (2010) distinguishes first- and second-order processes: the former is any process triggered by perceptual input, while the latter is any process that operates on a first-order processes and other processes that are more "interestingly cognitive", for example evaluating a stimulus (p.5). Shettleworth further describes how it is difficult for animal cognition researchers to distinguish *associative* processes, which are defined as those resulting from conditioning, from *nonassociative* processes which are "higher" processes that are not associative, including insight, representations, reasoning, or computations (p.19). It is difficult to identify mechanisms, such as first- or second-order processes, just from looking behaviour but certain qualities might give an indication. Humphrey (1972) remarked that the difference between looking at images for interest (seeking information) or pleasure (effect on well-being) is "operationally elusive" (p. 396), but noted that interest decreases over time as would interest-triggered looking behavior whereas pleasure elicits continued looking behaviour. Fujita and Matsuzawa (1986) found that a chimpanzee preferred scenic pictures that included unknown humans over scenic pictures without humans and concluded that this showed categorization ability. Preferring images from a category could be possible without a

sophisticated categorization process, however, as would be the case if attention to certain stimuli is hardwired. Identifying the mechanisms of preference may be difficult, but certain qualities such as strength of preference, whether it continues through prolonged exposure and/or whether it is maintained when attention is divided, and distribution of a preference across species and individuals, may all give clues to its causes and mechanisms.

Measuring spontaneous preferences

Measuring spontaneous behaviour removes the risk of training effects, reduces the chance of confounds, and ensures a degree of interest in the stimuli because, by definition, participation is voluntary. Using food rewards for a cognitive task may result in unintended outcomes. For example, D'Amato and Van Sant (1988) trained capuchin monkeys to select pictures with humans over pictures without humans, but upon further examination the pictures with humans had patches of red, a chance confounding characteristic, so that what appeared to be selection of pictures of humans may have been selection of pictures with patches of red. There is an inherent risk of not conceiving of, and controlling for, a feature that correlates with a stimulus category, especially since conceptual categories often overlap with consistent perceptual characteristics. While confounding features may occur in all research, they are less likely to affect a spontaneous paradigm because the lack of food reward prevents systematic conditioning as well as any behaviour directed at obtaining the reward. Preference or avoidance of certain colours or categories could confound results of non-preference research: a subject may choose a stimulus due to preference rather than the ability being tested (Murai et al., 2005; Tanaka, 1997). Marsh and MacDonald (2008) noted that Sumatran orangutans had systematic bias in errors when trained to select pictures of great apes: error trials often featured stimuli with salient characteristics such as striking facial features or bright colouration.

Preference measures: Passive looking-time versus active subject-controlled paradigms.

The looking-time paradigm measures preference as the amount of time that a subject spends looking at a target (Aslin, 2007; Winters, Dubac, & Higham, 2015). This is a passive task because the subject observes the stimuli without any control over stimulus presentation. In contrast, an active task requires a subject to perform a manipulation, such as pressing a button. Looking-time paradigms are used to assess numerous processes and cognitive abilities in human infants (Aslin, 2007) and other animals (Winters et al., 2015). For example, looking-time has been used to assess chimpanzee understanding of physical relations of objects (Cacchione & Krist, 2004), perceptual bias in rhesus macaques, humans, and dogs (Guo, Meints, Hall, Hall, & Mills, 2009), and facial processing and social preferences in several primates (*chimpanzee* Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005; *gibbon* Myowa-Yamakoshi & Tomonaga, 2001; *tamarin - Saguinus oedipus* Neiworth, Hassett, & Sylvester, 2007; *rhesus macaque* Waitt, Maestripieri, & Gerald, 2007). The looking-time paradigm is useful for comparing preference across species, and can be widely applied, even to young individuals and those lacking the dexterity or appendages to use a button, such as three-week-old domestic cats (Wilkinson, 1995). Thus, comparisons can be made across species and throughout development with identical or very similar methods and stimuli (e.g., Guo et al., 2009).

An active paradigm is an alternate method of measuring preference, in which the subject can control the duration of presentation of a stimulus using a touchscreen, button, lever, or similar apparatus. For example, picture preference studies with chimpanzees have used button pressing (Fujita & Matsuzawa, 1986) as well as touchscreens (Tanaka, 2007). Touchscreens provide a good opportunity to study preference due to the simplicity of design and immediate contiguity of touching the screen and viewing stimuli, and they have been used extensively with

animals and pre-linguistic human participants. For example, studies of Sumatran and Bornean orangutan cognition have used touchscreens to measure music preference (Ritvo & MacDonald, 2016), categorization (Marsh & MacDonald, 2008; Vonk & MacDonald, 2004), spatial strategy (Marsh et al., 2012), and memory (Renner, Price, & Subiaul, 2016).

Another important distinction in preference studies is the presence or absence of food rewards. Some studies reward all choices, other studies use non-differential reinforcement: rewarding at a predermined interval or ratio independent of subject behaviour (Anderson & et al., 2005; Humphrey, 1972; Lacreuse, Martin-Malivel, Lange, & Herndon, 2007; Tanaka, 2007). The addition of the food reward may change motivation and participation levels, potentially affecting the underlying construct measured, since intrinsic preference may differ from selection to receive a reward. Ritvo and Allison (2014) noted that if stimuli are unescapable, a selection may not only not indicate *liking*; instead, a choice might be an escape via the least aversive of the stimulus options. Use of rewards may similarly coerce participation, creating an inescapable condition for individuals with high food drive, resulting in behaviour that is motivated by reward rather than intrinsic interest. Therefore, data from rewarded and unrewarded preference experiments should be compared with caution.

Justification and current study

Preference has been measured using various methods, but the equivalence of these methods has not been verified. Although looking-time and touchscreen research may both aim to test the same construct of *preference*, a distinction is that the subject is passive in the looking-time paradigm and active in the subject-controlled paradigm. Passive and active designs could influence aspects of participation and attrition, and therefore research findings. It is possible that requiring an active behaviour could even alter the phenomena studied: as a passive look may

function according to a different cognitive mechanism than an active behaviour. Different outcomes have been reported in passive and active research paradigms for various cognitive tasks in human infant research (Charles & Rivera, 2009; Shinskey & Munakata, 2005). For example, research on object physical relations has showed differences across passive and active paradigms in human children (Hood et al., 2003) and rhesus macaques (Santos & Hauser, 2002). Human children showed longer passive looking-time at impossible events at a younger age than a parallel experiment which required actively reaching for an object (Hood et al., 2003). The passive task did not involve a delay so perhaps working memory demands were a confound for the active task, or perhaps the passive task required a prediction and the active task required an explanation, so these seemingly similar tasks engage different aspects of cognition (Hood et al., 2003). Rhesus macaques also showed longer looking-time at an impossible event in which an object passed through a solid shelf but were not successful in a corresponding active experiment on retrieving the object (Santos & Hauser, 2002).

Although there are excellent theoretical reviews of the looking-time paradigm by Winters and colleagues (2015) and Aslin (2007), little empirical work has been done to assess the use of looking-time and touchscreen use for animals. Hopper, Egelkamp, Fidino, and Ross (2018) found that a gorilla's (*Gorilla gorilla gorilla*) touchscreen choices for images of food matched manual food choices, supporting use of a touchscreen as equivalent to manual food preference tests. However, O'Hara, Huber, and Gajdon (2015) found that a kea (*Nestor notabilis*) showed better performance with real objects than a parallel task on a touchscreen. Comparing the validity, advantages, and disadvantages of different research paradigms is important to improve the quality of findings. Comparison of passive and active paradigms can also inform animal cognition research design more broadly, beyond preference, to evaluate suitability to different

species, populations, and research questions. If passive and active paradigms produce different findings this could explain discrepancies in the research literature.

The aim of this current study was to evaluate passive and active methods of assessing the preferences of captive Sumatran orangutans, using a traditional looking-time paradigm and a computer touchscreen. In Study 1, orangutans were presented comparisons of images using simultaneous slideshows on two laptop computers, and preference was measured by time looking at each image. In Study 2, orangutans had access to touch-sensitive monitor that displayed images whenever orangutans touched the screen. The amount of time the orangutans held each image on the screen was used as an indicator of image preference. For Study 3, rather than present images on a touchscreen, orangutans were simply shown pairs of printed images with a qualitative code of preferred side based on a subjective observation of looking-time and other behavioural indicators. For all three methods, the orangutans were shown photos with or without animals. This simple stimulus distinction was chosen because preference for images of animals has been reported across a variety of primate species (e.g., Fujita & Matsuzawa, 1986; Hanazuka et al., 2012), so it was likely that preference could be detected and assessed. Ability to discriminate animal from non-animal photos has previously been found in orangutans (Vonk & MacDonald, 2004) and a gorilla (Vonk & MacDonald, 2002). We assessed the level of voluntary participation by the orangutans as well as stimulus preferences using each method.

Study 1: Passive Looking-Time

Orangutans were shown photo slideshows simultaneously on two computer screens and looking-time was coded for different stimuli. Preference was defined as a bias in visual attention to certain categories of photographs. We predicted that the orangutans would show a preference for photos containing animals compared with photos not containing animals.

Method

Subjects. Initially eight Sumatran orangutans (*Pongo abelii*) from the Toronto Zoo were available, however only a subset participated in each study. Orangutans included Jahe (female 11), Molek (male 30), and three mother-offspring dyads: Puppe (female 41) and Budi (male 2.5), Ramai (female 23) and Jingga (female 1.5), and Sekali (female 16) and Kembali (male 2) (all ages in years). The orangutans had no previous experience in a spontaneous visual preference study but had viewed images in various contexts of zoo life, and some orangutans had participated in rewarded research with a touchscreen or printed pictures. Participation was voluntary and not reinforced. We conducted research in the off-exhibit enclosures in the context of the orangutans' regular schedule and environment. Orangutans had been partially segregated into holding areas and play rooms depending on fluctuating social dynamics, where they had access to climbing structures, bedding materials, and objects such as buckets and toys. The studies were designed to function concurrently as cognitive enrichment for the orangutans. Orangutans had *ad libitum* water and their diet was not altered. Research complied with ethical guidelines of Canada, York University, and the Toronto Zoo.

Apparatus. We displayed two slideshows simultaneously on two Mac PowerBook G4 laptops with 30.5 cm screens. The computers were placed on milk crates at a height of 28 cm, 50-100 cm from the caging, with a distance between the computers ranging from 30-60 cm. Distances were adjusted to account for differences in size of the adult and infant orangutans. Data were recorded by video cameras placed on tripods located between the computers. Images were presented in a slideshow using Microsoft® PowerPoint 2007. Each image was visible for 5 s. There was a sound-effect each time the image changed to alert the orangutan that the image had changed, and to confirm to the experimenters that the slideshow was progressing. To avoid

cuing, we remained behind the computers where we could not see the slideshows, and we were blind to the order of photos on the slideshows.

Stimuli. Stimuli were colour photographs enlarged to fill at least 80% of the screen, with background details included. We selected images from internet searches, and the zookeeper and experimenter's albums. Some of the control stimuli were created using Microsoft® PowerPoint 2007 and Photoshop CS3. Animal stimuli included both faces and whole-body images. The majority of the stimuli featured mammals, such as orangutans, humans, other primates and dogs, however there were also some marsupials, birds and reptiles. Non-animal stimuli featured objects of varied colour and detail such as cars, chairs, and trees, as well as some non-object stimuli such as shapes or a pattern (see **Appendix D** for a sample of the stimuli). Photographs were matched roughly for quality, clarity, and size, and target and control stimuli were sourced using parallel methods and search terms. The slideshows compared ten sequential images on each of the two computers simultaneously, with four shows, for a total of 40 animal images (target) and 40 non-animal images that each orangutan viewed once. Image presentation was counterbalanced with the target on the left and right screen.

Measures. Preference was operationally defined as longer looking-time at a stimulus category. Looking behaviour was coded from videotape by two observers blind to the location of the target and content of the slideshow. Interrater reliability had an overall Cohen's kappa of 0.81. The data were coded using the TakLin SubTrak Video Coding program (Takach & Lindtvedt, 2005). Looking-time was coded at 0.1 s intervals, similar to advancing a video frame by frame. At each 0.1 s interval the orangutan's eye orientation was coded as looking at the left screen, looking at the right screen, not looking/unclear, or blinking/eyes closed. After blind coding, the codes were transformed into the categories of stimuli by referring to a slideshow key.

The videotapes were also coded in real time using a categorical code of preferred side taking into account facial expression, posture, and other behavioural indicators. These categorical codes were consistent with the quantitative data.

Procedure. Orangutan participation was voluntary and not reinforced. While we set up the apparatus the orangutans typically moved to the front area of their enclosure, sometimes even gathering blankets and other bedding materials to make a day-nest in front of the computer, appearing motivated to participate. The testing session began when an orangutan was present in the front 2 m of the enclosure and continued until all stimuli had been shown. Data were included from any trials that met the minimum participation criterion: looking at each screen at least once within a trial and remaining within the front 2 m of the enclosure. We used three pilot sessions to assess the optimal positioning of the computers, duration that orangutans would maintain interest in this task, to habituate the orangutans to the researchers and apparatus, and to resolve technical issues. Training trials were not required because the study measured spontaneous behaviour. Statistics were performed using R version 3.5.1 (R Core Team, 2018), RStudio (RStudio Team, 2016), and lme4 (Bates, Maechler, Bolker, & Walker, 2015).

Results and Discussion

All orangutans had the option to participate; five of the eight met the participation criterion. The average rate of participation was 61%, calculated as time looking at screens out of time meeting the participation criterion. Participation varied between orangutan subjects: Budi 69%, Jahe 69%, Kembali 53%, Molek 81%, and Puppe 32%. Data points consist of each look at the computer screen by each orangutan, which may include multiple looks at a single image. We predicted that orangutans would show longer looking-times for images of animals than for non-animal images. For each comparison, time looking at a stimulus category was calculated.

Orangutans looked at animal stimuli on average 36.4 times with a mean looking time of 1.91 *s* (*SD* = 1.77), and non-animal stimuli on average 33.0 times with a mean looking time of 0.83s (*SD* = 0.83). The raw duration data were not normally distributed. Average duration was brief, and the data were positively skewed from a few long duration data points. Rather than eliminate potentially meaningful outliers, a log 10 duration was used for the remainder of the analysis. A repeated measures ANOVA was conducted with subject as a factor, to account for multiple data points from the five available orangutans. As shown in **Figure 3.1**, duration of looking-time was significantly longer for animal than non-animal stimuli $F(1,4) = 54.64$, $p < 0.001$.

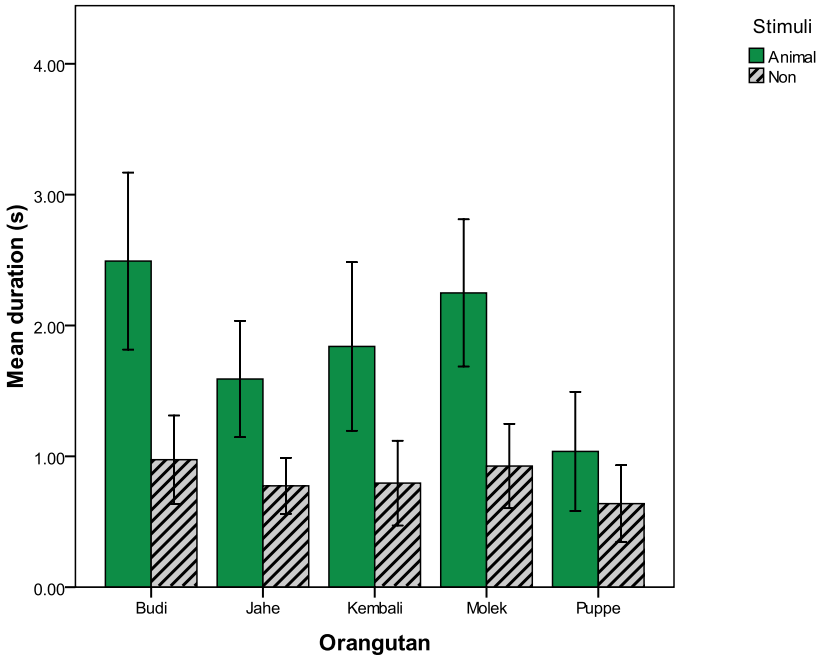

Figure 3.1. Looking-time: Average looking-time for animal stimuli (green) versus comparison non-animal stimuli (grey), error bars indicate 95% CI.

Preference for animal stimuli over non-animal stimuli was consistent with prior primate research (Fujita & Matsuzawa, 1986; Kano & Tomonaga, 2013; Hanazuka et al., 2012;

Humphrey, 1972; Myowa-Yamakoshi & Tomonaga, 2001). This can be considered support for use of a passive looking-time paradigm with orangutans. The majority of the orangutans participated, with varied levels of interest. A drawback of this method was the time-consuming task of coding video.

Study 2: Active Touchscreen

In this study, we compared performance in a passive looking-time paradigm to an active touchscreen task. Orangutans had access to a touchscreen computer that displayed a different image each time the screen was touched. The image was displayed as long as the orangutan maintained contact with the screen. A new image was displayed with each subsequent touch. The duration of time that the orangutan maintained each image on the screen was then calculated as a measure of image preference.

Method

Subjects. See Study 1 for a description of the orangutans, habitat, and conditions. This study took place two years after Study 1, so orangutans were two years older, Molek was deceased, and Jahe had been moved to another zoo. The three mother-offspring dyads remained (six orangutans). The three adult females had research experience with rewarded touchscreen studies (Marsh & MacDonald, 2008; Vonk & MacDonald, 2004), while the three young orangutans had not previously used a touchscreen.

Apparatus. We presented images on an iMac G4 computer with a 50.8 cm screen, with a Keytec “Magic Touch” touchscreen. The screen was placed 2-5 cm from the caging, 38 cm above the ground. The orangutans could touch the screen with their fingers, however they had previously developed a preference for using sticks to contact touchscreens. We provided wooden dowels and the orangutans opted to use the dowels to activate the touchscreen.

A computer program was created in Java SE 6 to display an image when the screen was touched. Stimuli were a total of 135 new images, 75 animal images and 60 non-animal images, procured and formatted as in Study 1. The image remained on the screen until the touch ended. A blank white screen was displayed whenever the screen was not touched. On each subsequent touch a new image was displayed. The program presented images in a random order to avoid order effects and continued until all images had been displayed. The identity and duration of touch for each photo was recorded by the computer program. Transition sounds indicated to the experimenter that the subject had touched the screen, and a final sound indicated that all images had been viewed.

Procedure. We began testing trials when the orangutan first touched the screen and continued until all images had been viewed, with 20 images per session. To account for inattention and cases where the orangutans ceased to participate, the show terminated when the screen had not been touched for one minute. We halted the trial if the subject departed or became agitated, or if there were any disruptions or noise from humans or other orangutans. If a session ended early the orangutan was provided two other opportunities to participate, either later that day or on a subsequent day, as per zoo schedules. We gave the orangutans a food reward at the start of each trial at the first touch of the screen, as well as at the end of the session for returning the dowel. To avoid cuing we were blind to the order of images, and remained behind the apparatus, out of view of the orangutans, and unable to see the slideshow. We conducted pilot trials to introduce the orangutans to the apparatus and procedure, and to resolve technical difficulties.

Results and Discussion

Of the three mother-offspring dyads available (six orangutans), only two mothers (Ramai, Sekali) and one young male (Budi) participated. Ramai and Sekali monopolized the apparatus, keeping their infants from participating. Puppe, the mother in the third dyad, had low interest in participating, but her infant, Budi, participated. The orangutans showed a moderate level of interest. The total number of images viewed by each orangutan equaled the number of screen touches: Budi 88, Ramai 123, and Sekali 108. The mean duration of touch for animal stimuli was 2.53 s (*SD* = 6.62), and for non-animal stimuli 1.14 s (*SD* = 1.34). As with Study 1, the log 10 duration was used, and stimuli were compared using a repeated measures ANOVA with subject as a factor. As shown in **Figure 3.2**, the duration of screen touch was significantly longer for animal than non-animal stimuli $F(1,2) = 10.774$, $p = 0.0011$.

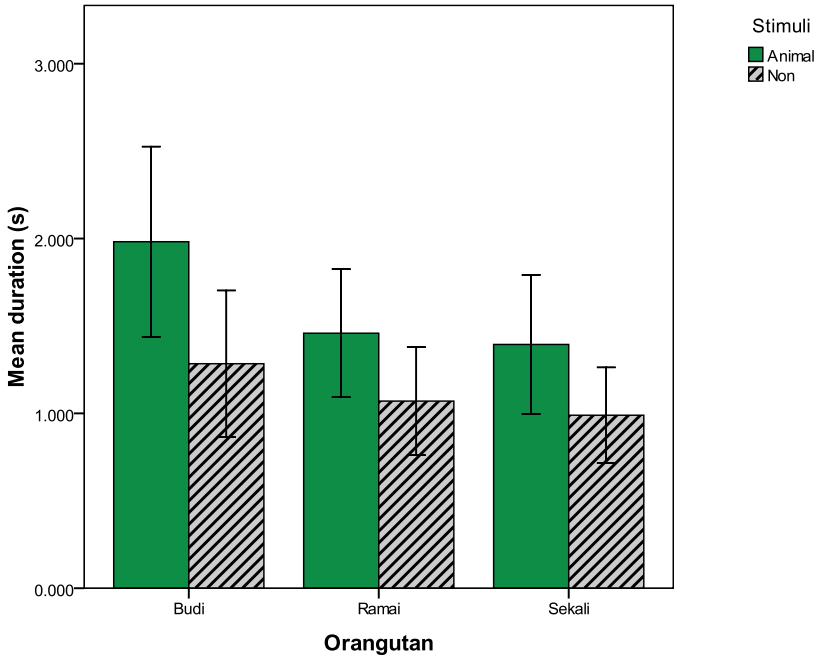

Figure 3.2. Touchscreen: Average duration of touch for animal stimuli (green) versus comparison non-animal stimuli (grey), error bars indicate 95% CI.

As predicted, orangutans preferred images with animals over non-animal images. This was consistent with Study 1, showing reliability across passive and active research paradigms. Participation rates were lower than in Study 1 due to individual differences and social factors, so studies using a touchscreen should factor in these potential constraints on data collection. To further evaluate passive and active paradigms, in Study 3 we examined the same preference for animal over non-animal stimuli using a simple flash-cards method.

Study 3: Passive Flash-Cards

Study 3 was a third preference test by simply holding up printed images with live categorical coding of data, to serve as a quick and easy method to obtain a measurement of passive preference. This method was conceptually similar to that used in Study 1 but did not use a computer to present the images. Thus, it provided a cheap, low tech alternative that could be used by animal husbandry staff in a variety of captive settings.

Method

The potential subjects were the same as those in Study 2, with six orangutans available to participate. We showed orangutans a series of comparisons of two images. Colour images were printed on letter paper, cut to 12 x 16 cm, and then two images were attached to a large piece of cardboard side by side, separated by 7-9 cm. We displayed the two images simultaneously: one included an animal (target) and a second image did not include an animal (comparison). Stimuli were held at a distance of approximately 30 cm from the orangutans. Location of the target (left or right) was randomized across trials. Orangutans could view 108 flash-card comparisons.

An observer blind to the location of the target stimulus coded preference. On each trial the observer held up a two-image comparison for the orangutan to view, and the preferred stimulus side was coded live. The observer called out the preferred side (“left” or “right”) while

remaining blind to the location of the target and the content of the stimuli. The preferred side was coded using a forced-choice paradigm, in which the observer must make a judgement on all trials (Teller et al., 1974). The observer evaluated the orangutan's preference by incorporating a subjective observation of the frequency and duration of look, as well as other behavioural indicators such as posture, leaning closer to one screen, "double-take", looking away abruptly, and affective behaviours such as facial expressions and vocalizations. A research assistant recorded the stated code, and then the cardboard was flipped over to reveal the stimuli to the coder, similar to a "flash-card". Trials were excluded prior to stating a code if there was a disruption or error, for example, if there was an interruption by another orangutan. Participation was voluntary and no food rewards were provided. The study measured spontaneous behaviour, so no training phase was necessary although we removed the first three sessions from data analysis as practice.

Results and Discussion

All six available orangutans voluntarily participated in this study. There was participation by all subjects during all research sessions with one exception, a day when construction noises on the roof caused the orangutans distress. Orangutan participation was high; of the possible 108 flash-cards orangutans viewed an average of 88% (M = 95/108 flash-cards, SD = 5.65, ranging 85-101). Data were categorical: each trial was recorded as one stimulus *preferred* over the other.

The frequency of preference for animal stimuli and non-animal stimuli was tabulated for each orangutan, and then these totals were compared across orangutan subjects using a paired samples t-test. Overall, the orangutans significantly preferred animal stimuli (M = 70.17, SD = 14.25) over non-animal stimuli (M = 24.33, SD = 12.29); $t(5) = 4.317$, $p = .004$, 95% CI [18.54, 73.12], $d = 1.76$ (1-tailed) (**Figure 3.3**).

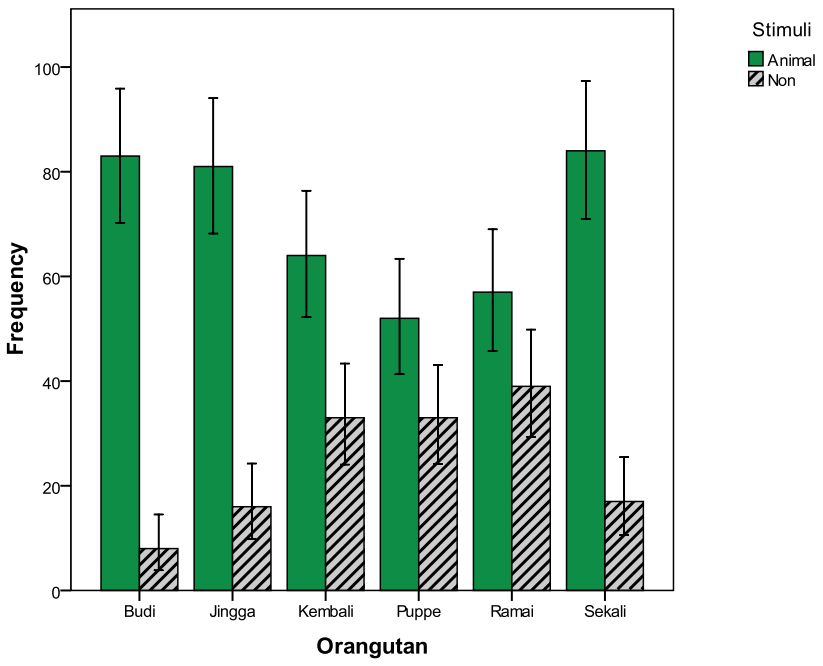

Figure 3.3. Flash-cards: Frequency of preference for animal stimuli (green) versus comparison non-animal stimuli (grey), error bars indicate 95% CI.

The orangutans preferred animal over non-animal stimuli, consistent with the findings of both Study 1 and Study 2. The high level of participation may be attributed to the low effort required; orangutans simply had to pass by and glance at the images. The benefit of easy data collection was offset by the drawback that data from this task were categorical, thus not allowing for more sophisticated analysis of the magnitude of preference.

General Discussion

Looking-time, touchscreen, and flash-card methods were compared according to level of interest and voluntary participation by the orangutans, the ability of each task to detect preference, and the theoretical and practical considerations of each paradigm. The studies were designed to measure the same cognitive property of "preference", using passive looking

behaviour and active touchscreen behaviour. Careful analysis of the assumptions of the passive looking-time paradigm (Aslin, 2007; Winters et al., 2015) and active apparatus is important to avoid anthropomorphic assumptions that an animal will use and interpret a technology in a similar way to humans, who approach a computer with prior knowledge and expectations (Ritvo & Allison, 2014).

Orangutan interest and use of the apparatus

All three studies relied on voluntary participation, so a degree of intrinsic interest, curiosity, or rewarding properties were required for the apparatus to function. The looking-time study had an intermediate level of participation (5/8 orangutans), the touchscreen study had the lowest participation (3/6 orangutans), and the flash-cards study showed the highest participation (6/6 orangutans).

Five orangutans participated in the looking-time study, looking at the slideshow screens with moderate interest. The three adult females had the lowest level of participation. These orangutans had young infants at the time of study, which may have held their attention and decreased their need for enrichment. Molek (adult male) had the highest participation. Dinding, an adult male orangutan (50 years), also exhibited a high level of interest in the slideshows but passed away during the pilot stage of the study. We excluded Dinding as a subject when his health began to fail; however, Dinding was agitated when he did not have the opportunity to watch the slideshows and performed a *long call* vocalization. In consultation with the zookeepers we resumed showing the slideshows to Dinding for enrichment purposes only, and he exhibited positive affect when he had the opportunity to watch. This further underscores the value of pictures as enrichment for some individuals. Bloomsmith and Lambeth (2000) found chimpanzees housed alone had higher interest in watching television than those housed socially.

This is consistent with the high interest by the adult males in our study, as they were housed alone in the off-exhibit enclosures. The high interest from adult males in our looking-time study conflicts with Boostrom (2013), who found adult males had the lowest participation in a study using an iPad. This difference could be attributed to several factors including individual and social differences, the topic of the stimuli, or the fact orangutans needed to actively touch a screen in Boostrom's study rather than passively watch the screens in our study. Unfortunately, no adult males were present for our study using a touchscreen.

Three individuals participated in the touchscreen study. The lack of participation by young Jingga and Kembali was due to their mothers monopolizing the apparatus. The low number of participants may reflect the difficulties of using a single apparatus with socially housed individuals. A study of a computer enrichment program found that Bornean orangutans would monopolize the computer and increased aggression (Tarou, Kuhar, Adcock, Bloomsmith, & Maple, 2004). However, another study did not find negative effects of a computer for socially housed orangutans (*Pongo sp*.) (Perdue et al., 2012).

The flash-card study had the highest participation rate of the three studies. Some orangutans approached more quickly and looked more intently at the stimuli, particularly Budi (young male) and Jingga (young female). Budi had high interest in interacting with researchers, as the researchers were closer with the flash-cards apparatus (holding the card by hand), this may have motivated Budi. Despite a motivation to interact with the researchers, Budi has exhibited low attention in prior research, often not meeting criterion for a simple discrimination (e.g., Adams, Wilkinson, & MacDonald, 2017). This may demonstrate an individual difference in the types of activities Budi is motivated to participate in. Herrelko, Vick, and Buchanan-Smith

(2012) found that personality, especially a measure of *openness to experience*, predicted zoo chimpanzee participation in a touchscreen task.

Comparison of methods: design, best practices, and practical considerations.

The looking-time paradigm showed the predicted preference for animal stimuli over non-animal stimuli. This paradigm has not been evaluated empirically for use with animals, although Winters and colleagues (2015) present an excellent review of the looking-time paradigm for animals noting advantages such as ability to test cognition in pre-linguistic infants, as well as important criticisms including overinterpretation of data and lack of proper controls. Aslin (2007) also reviewed the looking-time paradigm for infant research, observing that specific cognitive mechanisms cannot be inferred from looking-time because the same duration of look can be produced by very different cognitive mechanisms and contexts (see also Humphrey, 1972). In the most conservative approach, no cognitive state can be inferred from looking-time, an issue discussed in philosophy under the *problem of other minds*. Andrews (2015) outlined the assumptions we employ in the habituation looking-time paradigm for human infants: that an infant will look away from a stimulus once bored, that a longer look at a new stimulus indicates differentiation of stimuli, and that a short looking-time for repeated viewing of a stimuli indicates recognition.

The touchscreen study was an active apparatus, in contrast to the passive looking-time and flash-card studies. To humans it may be intuitive to equate holding a preferred image on a touchscreen to a prolonged look at a preferred image. However, looking behaviour versus touchscreen behaviour may not be equivalent for a nonhuman primate, and the two behaviours may not have the same outcomes when measuring a variable such as preference. Adding an active behaviour such as touching the screen (or pressing a button), requires an intermediate step.

Operant conditioning should quickly link the behaviour of touching the screen with the consequence of seeing an image. However, touching a screen is not as simple a measure of preference as looking, because learning, reaction time, and motor ability could introduce error. For example, an experimental device allowed human infants to control how long pictures were displayed by turning their head; this method did not detect preference for pictures of smiling humans over blue slides, but coded looking-time did detect the predicted preference (McLaughlin, Deni, Drake, Borrebach, & Cavallaro, 1978). There are reports of discrepancies between passive and active paradigms in human infant and child research, and it is possible that there are many more cases in which conflicting research findings can be attributed to these differences in apparatus. Anderson and colleagues (2005) report different outcomes when a touchscreen versus printed stimuli were used to measure capuchin and squirrel monkey preference, despite the two apparatuses using the same pictures. Therefore, verification across passive and active experimental apparatus or other aspects of research design can reveal that a different apparatus may not show the same result or measure the same property.

Pictures with animals were preferred over pictures without animals in all three studies, as was expected. This can be considered support for convergence of methods with the passive apparatus and active apparatus. Further, it is evidence that the mechanism of preference is not always vulnerable to disruption by an active behaviour, differing from research showing a dissociation in passive and active tasks. Touching the screen could potentially employ a more cognitively complex behaviour than looking at a screen, if the looking behaviour could be reflexive. Differences between passive and active tasks may then offer clues to mechanisms. More goal-oriented voluntary behaviours, such as deliberately wanting to see a picture of an animal, might be more resistant to change across paradigms, so perhaps this is evidence that

preferential looking at animals is not just a reflexive look, and that it is sufficiently reliable to be detected in different contexts using different tasks.

As an enrichment tool, the touchscreen apparatus is advantageous because it provides orangutans control and choice of stimuli. Control and choice are two key factors found to increase welfare and psychological well-being in captive nonhuman primates (Buchanan-Smith, 2011; Washburn, 2015). This was our original intention with the touchscreen program: given the amount of time that humans spend voluntarily looking at photos on social media, perhaps the orangutans would have a similar interest in viewing photos. However, Ritvo and MacDonald (2016) found that well-meaning attempts at enrichment may be aversive to subjects, so careful implementation is important to ensure an enrichment device or research apparatus is beneficial and suitable. Perhaps different photographs or conditions may have elicited more interest by the orangutans, or enjoyment of photos may vary across primates.

The data coding and characteristics differed across studies. The Study 2 touchscreen data was coded automatically by the computer program, which was efficient and removed the chance of observer bias. However, it risked that screen touches were not measuring preference, as orangutans could look away distracted while maintaining touch with the screen or could accidentally end a touch while still interested in an image. In Study 1, looking-time data were coded from videotape, which was very time consuming but provided a precise measurement of look duration and allowed for verification. The qualitative data from Study 3 allowed for the quality of looking behaviour to be weighted, for example, an intense look versus disinterested gaze. It was also less time consuming, so it may be advantageous for pilot testing stimuli.

Eye-tracking technology would obviously result in more precise measurement of orangutan looking times, but this technology typically requires the participants to either wear a

headpiece or remain relatively still, neither of which was feasible for these zoo-housed animals. Advances in eye-tracker technology may reduce these requirements, improving feasibility for use with captive apes (Kano & Tomonaga, 2013). Future studies may combine coding methods, for example a touchscreen or eye-tracker for precise measurement of duration, as well as a qualitative code from videotape to assess the quality of looking and attention. Following this research, a study was conducted to measure the music preferences of these same subjects, and they preferred silence and reacted with agitation (Ritvo & MacDonald, 2016). If the computer sounds had similar effects it could have influenced participation or created a distraction so we recommend that future studies carefully consider any noise that their apparatus produces.

Summary and conclusions

The passive looking-time and active touchscreen paradigms have potential for excellent data collection depending on the context. Aspects to consider before implementing an apparatus are group dynamics, methods of ensuring attention, and dealing with outliers. The flash-card study had a high participation rate and could be considered a simple method that is resistant to technical malfunctions, and useful in piloting and ruling out stimulus bias confounds, although this method is less precise for more specific research questions. The looking-time apparatus was an appropriate method for these subjects, produced useful data, had moderate participation, and would be ideal if eye-tracking technology could replace the time-consuming coding from videotape. The active touchscreen apparatus has the potential to collect data with precise timing, however careful consideration of the motivation of the participants and group dynamics are required. The convergence of results across passive and active methods suggest that both can be useful tools to explore orangutan cognition. Looking-time and touchscreen methods have been used extensively but had not yet been empirically evaluated, so our findings are reassuring that these tasks are appropriate for orangutans. When provided images that were

likely to be of interest, orangutans looked longer, and actively touched a screen for longer. This supports the likelihood that orangutans may interact with photos as we would, both while passively and actively viewing images of interest. In this context we found that orangutans, like humans, appear to be intrinsically motivated to view photographic images.

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CHAPTER 4

Adams, L., Wilkinson, F., & MacDonald, S. E. (2017). Limits of spatial vision in Sumatran orangutans (*Pongo abelii*). *Animal Behavior and Cognition*, *4*(3), 204-222.

Note. With input from my dissertation committee, Chapter 4 differs from the published version in the following minor ways. The section titled "Orangutan life history" has been revised to be titled "Orangutan evolution and selective pressures". Two sentences were added to note the possibility that the two orangutan subjects are not good representations of the species, due to chance or some aspect of their living conditions. There were also changes to word order and word choice for the purpose of clarity that did not change the overall meaning of the sentence. The first table in the paper has been changed to be **Appendix E** because the page is oriented to landscape.

Abstract

Although research with animals is often done under the assumption that visual abilities are similar across species, the visual ability of most animals, including orangutans, has not been experimentally evaluated. In this study we assessed the contrast sensitivity function (CSF) of two female zoo-housed Sumatran orangutans (*Pongo abelii*) aged 20 and 26 years old. Orangutans were rewarded for selecting vertical or horizontal square wave gratings at the correct orientation. Results showed a CSF similar in shape and position to that of human adults, although with lower contrast sensitivity. These lower values may be due to testing constraints or may be due to species differences. These data have implications for research on orangutan cognition, hominid evolution, and have practical implications for captive and wild management of this endangered species.

Limits of spatial vision in Sumatran orangutans (*Pongo abelii*)

Primate vision shows similarities and differences across taxonomic and geographic divides as well as across habitat, life history, and ecological niche (Matsuno & Fujita, 2009; Veilleux & Kirk, 2014). For example, there are differences in color vision and visual acuity across nocturnal, diurnal, and cathemeral primates (Jacobs, 1977, 1996; Kirk, 2004; Matsui, Go, & Niimura, 2010; Ordy & Samorajski, 1968; Veilleux & Kirk, 2014). Eye morphology and visual system anatomy and physiology are similar within Old World monkeys and apes, but differences exist between these species and New World primates (Chan & Grünert, 1998; Waitt & Buchanan-Smith, 2006), and between haplorhine and strepsirrhine suborders of primates (Kirk, 2004; Veilleux & Kirk, 2009). Our closest relatives are the other great apes, yet there is limited information about either behavioural or physiological aspects of vision in these species. Orangutans are often assumed to have identical vision to humans, and this assumption underlies cognitive testing with the species. However, there are few published reports of orangutan visual ability, and no reports of the orangutan contrast sensitivity function. The purpose of the present study was to examine basic spatial vision limits in orangutans.

Orangutan evolution and selective pressures

Orangutans are an important species to study to understand great ape evolution because this genus had an early phylogenetic divergence from the African great ape lineage and geographic isolation in Asia. Evaluations of human phylogenetic relationships typically cite a common ancestor with chimpanzees (*Pan troglodytes*) 6 million years ago (MYA), and a common ancestor with orangutans 14 MYA (Goodman et al., 1998). Orangutans also provide a valuable comparison to other great apes due to differences in their ecological niches. They spend more time in the tree canopy in comparison to other great apes and live predominantly in

lowland areas, including peat swamps (Rijksen, 1978; van Schaik, 2004). This habitat is characterized by low-level light conditions, with mottled light that has been filtered through the leaves of the forest canopy. In these conditions orangutans must find food, which can be difficult to identify and can require extensive travel to locate (Rijksen, 1978). The majority of the Sumatran orangutan diet is fruit, but they also consume bark, leaves, pith, flowers, sap, roots, seeds, honey, fungi, mineral-rich soil, eggs, invertebrates, and meat, and obtaining and/or preparing some of these foods required precise manipulation and tool use (Hardus et al., 2012; Rijksen, 1978; van Schaik, 2004; Wich et al., 2004). Like other diurnal primates, vision is orangutans' dominant sense, and they rely on it to locate and identify these foods (Gilad, Wiebe, Przeworski, Lancet, & Pääbo, 2004; Matsuno & Fujita, 2009; Schrauf & Call, 2009). Vision is also crucial for arboreal travel. Because orangutans are large and heavy in comparison to other arboreal animals, accurate estimation of distance and quality of branch support is essential in preventing potentially fatal falls (Schmitt, 2010; van Schaik, 2004). Orangutan vision is also necessary for other aspects of daily life that require perception of fine detail and subtle contrast differences including tool use and viewing social partners (Rijksen, 1978; van Schaik, 1999, 2004), which they often perform in low light and in the forest canopy.

The orangutan eye and brain

There are no reported empirical tests of orangutan vision other than a study showing that a Bornean orangutan could discriminate grey paper in comparison to red, blue, green, and yellow (Tigges, 1963). However, there have been some preliminary anatomical measurements of orangutan eyes and visual cortex. Hotta (1905) reported detailed measurements of the globe and retina of orangutans, chimpanzees, gorillas (*Gorilla sp.*) and gibbons (*Hylobates sp.*) and confirmed the presence of a fovea in all these species. In more recent studies, Kirk (2004, 2006)

reported comparable measurements in one Bornean orangutan: mean transverse eye diameter of 22.8 mm, axial eye diameter of 22.6 mm, transverse corneal diameter of 11.6 mm, and an orbital aperture diameter of 36.1 mm, values similar to those of a chimpanzee (23.0, 21.8, 10.2, and 30.8 mm respectively). Montiani-Ferreira et al. (2010) noted that, while current knowledge about orangutan ocular anatomy and physiology is limited, orangutan eye physiology is similar enough to human eye physiology that human doctors were able to perform successful cataract surgery on a captive Bornean orangutan. Post mortem anatomical examination of the connections of short wavelength-sensitive (SWS) cones and horizontal cells in the retinas of a Bornean orangutan and a chimpanzee revealed similarity to humans in terms of the pattern of H1 versus H2 horizontal cell connections (Chan & Grünert, 1998). However, no other information about orangutan retinal organization is available.

An excellent general description of the orangutan brain compared to those of other great apes and humans is provided by Zilles and Rehkämper (1988). They concluded that, in terms of gross features and a scale of encephalization, the orangutan is most similar to the gorilla with both these species showing lower indices of telencephalic and cortical development than gibbon, chimpanzee or human. In the only recent studies we are aware of in which orangutan visual cortex was investigated (Preuss, Qi, & Kaas 1999), the dense band of cytochrome oxidase staining seen in layer 4A of Old and New World Monkeys was absent in human, chimpanzee and orangutan. On the other hand, a clear difference was seen between human V1 tissue and that of both the other great apes and the monkeys in terms of the pattern of presumed M-pathway targets in Layer 4A as revealed by immunological staining (Preuss et al., 1999, Preuss & Coleman, 2002). Finally, a recent study using post-mortem MRI measurements reported LGN and V1 volumes for three orangutans along with other great apes (De Sousa et al., 2010), and a second

study of sectioned material from the same animals made cytoarchitectural comparisons of several cortical areas, including V1 across all the great apes (Semendeferi et al., 2011). Beyond these studies nothing is known of orangutan central visual pathways.

Limits of primate visual ability

Visual systems can be characterized in terms of the limits of their ability to encode spatial, temporal, and wavelength information about the changing visual environment. Extensive laboratory-based behavioural and physiological studies exist that compare human visual systems to the most frequently studied non-human primate species, macaques, looking at all three of these properties, but information is much more limited for the full range of primates, and particularly for nonhuman great apes. Spatial vision has been most widely investigated, followed by color vision (for a review see Matsuno & Fujita, 2009). Data on temporal processing (motion and flicker sensitivity) is largely lacking in nonhuman primate species outside macaques (*Macaca fascicularis*) (O'Keefe & Movshon, 1998) and chimpanzees (Matsuno & Tomonaga, 2006b, 2008), yet is likely to be a critical sensitivity for skills such as arboreal travel.

Spatial vision refers to the ability to distinguish changes based on luminance variation across the visual field and to use these changes as a basis for constructing a representation of the layout and identity of objects in the visual scene. The contrast threshold refers to the minimum detectable difference in luminance between adjacent spatial regions. It is typically measured in the laboratory using a periodic pattern of parallel lines (a square or sine wave grating) and systematically reducing the luminance difference between the lighter (initially white) and darker (initially black) bars until they are an indistinguishable middle grey. Contrast sensitivity (CS) is the reciprocal of contrast threshold. However, CS varies as a function of the width of the bars and the viewing distance, which together determine the angle subtended at the eye by the

stimulus (visual angle) and the size of the resulting retinal image. For periodic stimuli such as gratings, this measure is expressed as spatial frequency (SF) or the number of cycles of grating making up one degree of visual angle (c/deg). The contrast sensitivity function (CSF) comprises the CS limit across the range of visible spatial frequencies. Under high luminance and optimal conditions, human and macaque CSFs show peak sensitivity between 2 and 5 c/deg with CS decreasing at lower and higher SF (Arundale, 1978; Boothe, Kiorpes, Williams, & Teller, 1988; Campbell & Robson, 1968; De Valois, Morgan, & Snodderly, 1974; Ross, Clarke, & Bron, 1985; Williams, Boothe, Kiorpes, & Teller, 1981; see **Appendix E** for a summary of CSF findings in primates). Sensitivity values at the peak range from 150 – 300 (contrasts of 0.3 – 0.6%) under optimal test conditions in these studies. The only study of CS in a non-human great ape (Matsuno & Tomonaga, 2006a) reported CSFs similar in shape although slightly lower in absolute sensitivity in four chimpanzees compared to the one human observer tested in the same apparatus. However, the location of the peak and the value of peak CS in this study were considerably lower than most values reported in the literature for human subjects (Arundale, 1978; Ross et al., 1985).

The highest frequency (finest lines) at which a grating can be detected at maximum (100%) contrast is the spatial resolution or visual acuity limit. This limit, when extrapolated from a measured CSF, corresponds quite closely to acuity measures obtained by more traditional means, namely reducing the SF/size of high contrast grating or other pattern until the stripes or gap cease to be detectable (Jacobs, 1977; Langston, Casagrande, & Fox, 1986). When contrast is maximized, humans, pigtailed macaques (*Macaque nemestrina*), and long-tailed macaques (*Macaca fascicularis*) can distinguish over 30 c/deg, with acuity estimates averaging 35 – 50

c/deg (Arundale, 1978; Boothe et al., 1988; De Valois et al., 1974; Ross et al., 1985; Williams et al., 1981).

Visual acuity rather than contrast sensitivity has frequently been used as a basis for describing the visual ability of a species and for cross-species comparisons. For example, Veilleux and Kirk (2014) have described the relationship between acuity and eye size and shape, and related this to habitat considerations. However, practical as well as theoretical considerations led us to choose CS as our measure. Practically, in order to measure acuity it is necessary to have available a range of stimuli that tightly bracket the SF range in which the threshold is likely to fall. Based on overall anatomical, ecological, and behavioural similarities to the other great apes, we expected that the visual acuity of the orangutan might be very high (35 – 50 c/deg) because values in this range have been reported in chimpanzees (Bard, Street, McCrary, & Boothe, 1995; Spence, 1934; Weinstein & Grether, 1940), as well as in humans, as discussed above. Producing adequate acuity stimuli for human subjects is not difficult because very long viewing distances can be used; clinical eye charts, for example, are typically used at a viewing distance of 20 ft. However, it is difficult to train non-human species on tasks without close spatial contiguity between stimulus, response, and reward (see Cowey & Ellis, 1967, for discussion of this issue). For animals with much lower visual acuity (< 8 c/deg), this can be successfully achieved using the Lashley jumping stand, in which the animal jumps toward a visual pattern (lemur *Eulemur macaco flavifrons:* Veilleux & Kirk, 2009; gerbil *Meriones unguiculatus:* Wilkinson, 1984), or as in the Mitchell adaptation for cats (*Felis catus*), jumping down onto a patterned surface (Mitchell, Giffin, Wilkinson, Anderson, & Smith, 1976). However, it is extremely difficult to produce, either by digital printing or electronically, a grating pattern as fine as 50 c/deg when within reach of the subject. In a highly constrained laboratory situation, it is possible to create the

impression of such contiguity by having the animal look through a mask or through push-panel windows toward stimuli placed at some distance at the end of tunnels, which mask out all other visual stimulation. However, this was not feasible in a zoo setting. To give the reader an understanding of the fine scale of patterns needed to reach human or macaque acuity limits at close range, imagine painting a set of 50 pairs of precisely equally wide black and white lines across the width of your fingernail, and then hold the finger at arm's length from your eye. Such a pattern is exceptionally difficult to produce and impossible to calibrate. So practically, it was more feasible to measure contrast thresholds using lower frequency (2 – 15 c/deg) printed patterns that the animals could physically contact.

There are also theoretical reasons to measure CS rather than acuity. The CSF is now understood to reflect the envelope of sensitivities of multiple spatial channels within the visual pathway, carrying information at several different spatial scales (Campbell & Robson, 1968; Lesmes, Lu, Baek, & Albright, 2010; Wilson & Giese, 1977) and thus, gives a more complete picture of spatial sensitivity. CSFs have been measured in a wide range of species including cats, pigeons, several rodents and several primates (see Uhlrich, Essock, & Lehmkuhle, 1981, for review, and **Appendix E** for primates), and the general form of the CSF is similar across species, if normalized for maximum sensitivity and scaled in terms of distance from the peak frequency in octaves (factors of 2) (Uhlrich et al., 1981). Because acuity is simply the limit of the CSF – the SF beyond which even 100% contrast patterns cannot be resolved, it can be extrapolated from the CSF provided enough values are tested to adequately determine the shape of the function. Finally, it has been argued that the CSF has more relevance to daily life than acuity (Owsley & Sloane, 1987), and this is likely also true for orangutans. Very few meaningful stimuli in the animal's natural world occur at extremely high SF and 100% contrast. Most stimuli of

importance in daily life, for example, the facial expression of a conspecific or a branch while brachiating, entail lower contrast and spatial frequencies well below the acuity limit.

Purpose and approach of the present study

When the possibility of evaluating spatial vision in Sumatran orangutans at the Toronto zoo emerged, there were both theoretical and practical reasons to do so. Visual stimuli have been used in cognitive experiments with orangutans to assess abilities such as memory (Swartz, Himmanen, & Shumaker, 2007), numerosity (Vonk, 2014), categorization (Marsh & MacDonald, 2008; Vonk & MacDonald, 2004), spatial cognition (Marsh, Spetch, & MacDonald, 2011), and language and symbol use (Miles, 1990), yet there was no basis other than assumed similarity to human visual ability to guide stimulus design. Secondly, assessment of orangutan vision has practical application in regards to zoo management and veterinary baselines, especially important for maintaining this Critically Endangered species (Singleton, Wich, Nowak, & Usher, 2016). And more theoretically, evaluating continuity and discontinuity in abilities across great apes, other primates, and other animals, can inform our evolutionary understanding of ancestral Hominoidea and primates in general.

The limitations of the zoo environment precluded the use of the highly controlled stimulus presentation sources used in earlier CSF and acuity studies of humans and other diurnal primates. In any case, the technologies generally used in the past (analogue oscilloscope displays, Ives visual acuity tester) are now obsolete and hard to obtain, and modern digital displays present other challenges in terms of luminance calibration. Instead, we turned to methods developed in laboratory studies of preverbal children and animals using hard-copy stimuli. Whereas many CS studies have been based on the discrimination of grating patterns from a matched homogeneous grey, it is difficult to obtain perfect luminance matches with

printed stimuli. Instead, we chose to use the more difficult discrimination between vertical and horizontal grating patterns, which allowed us to use the same physical stimuli as either vertical or horizontal simply by rotating them. Because of the need for stimulus-response spatial contiguity, we used a set-up in which the orangutans could physically touch the stimulus. Our goal was a modest one – to measure contrast thresholds at several spatial frequencies that would include values close to the peak of sensitivity, and values at frequencies that we anticipated might fall on the declining portion of the CSF, thus allowing us to plot the shape of the function. This, we hoped, would allow us to extrapolate an acuity estimate even though it was beyond our capabilities to create sufficiently fine grating patterns to capture the resolution limit of the system. Despite limitations encountered in producing extremely low contrast gratings, we were successful in achieving contrast threshold measures in two orangutans, which we compare to human participants, and to existing chimpanzee data (Matsuno & Tomonaga, 2006a).

Method

Subjects

Two of six Sumatran orangutans (*Pongo abelii*) residing at the Toronto Zoo at the time of this study participated in the study. All six orangutans were screened; however only two reached the initial training criterion within three months of training. The two subjects were both captive-born adult female orangutans. Sekali was 20 years old and Ramai was 26 years old. The study was conducted in the context of the orangutans' regular schedule and environment, and participation was completely voluntary. Orangutans had *ad libitum* access to water and their diet was not altered. Data were collected in the off-exhibit holding enclosures where there were climbing structures, bedding materials, and items for behavioural enrichment such as buckets and toys. The orangutans could also see and hear their conspecifics, so motivation and participation

fluctuated due to these distractions. This study complied with the ethics and research protocols of York University and Toronto Zoo, and the laws of Canada.

Apparatus and Stimuli

Stimuli were presented to the orangutans on a wooden display unit measuring 57 x 45 x 42 cm. The display unit had two podiums (left and right), which held the stimuli 17 cm apart (**Figure 4.1**). The unit also had a movable panel to obscure the orangutan's view of the stimuli in between trials. Once the orangutan was sitting, the unit was placed so that the stimuli were at a distance of 57 cm from the eyes of the orangutan. This distance was verified frequently, and remained constant because the orangutans held their faces against the mesh of the enclosure. If the orangutan moved or changed position, the location of the apparatus and distance were readjusted and confirmed. The orangutans used a wooden dowel to select the stimulus.

Figure 4.1. Stimulus display unit. During testing the stimuli were centered on the podiums with one oriented horizontally and one oriented vertically.

We created square wave grating stimuli using Adobe Photoshop CS5 computer software, printed them on non-glossy photo paper using a Canon Pixma MG6220 ink jet printer, and cut them into 12 x 12 cm squares. At a distance of 57 cm from the orangutan's eyes, one centimeter is equivalent to one degree of visual angle, so each stimulus subtended 12 x 12 degrees of visual angle. The target and comparison stimuli did not differ; they were taken from the same set of printed gratings. On each trial, two stimuli were selected from the set and placed on the display unit with one oriented vertically and the other horizontally. We printed a new set of stimuli for each testing day to ensure that there were no identifying marks on the stimuli. The orientation and/or the position of the stimulus cards was shuffled between trials so that across trials individual cards appeared as both target and comparison, and on both left and right podiums. Stimuli were replaced immediately if any identifying marks occurred.

The stimuli were printed for 2, 4, 10, and 15 c/deg when viewed at a distance of 57 cm. A set of lower frequency stimuli (0.5 c/deg) was produced for training purposes. We printed each of the four spatial frequencies at seven levels of contrast. Contrast values ranged from the highest to the lowest contrast that could be produced by the printer and computer software. The actual contrast values of the stimuli were obtained from luminance measurements made with a Minolta LS-100 photometer (**Table 4.1**). Maximum and minimum luminance values were used to calculate the Michelson contrast as follows: $\frac{L_{max} - L_{min}}{L_{max} + L_{min}}$. The photometer was used to measure the Michelson contrast in multiple locations within the testing area over two days and showed reliability in the values across locations and days. Contrast sensitivity (CS) was calculated as the reciprocal of the threshold (*CS* = 1 / *Contrast Threshold)*. The overall average luminance of all stimuli was similar, ranging between 19 – 22 cd/m^2 across stimuli.

Table 4.1

Average Michelson Contrast Values for Stimuli

Staircase Step	Michelson Contrast	SD	Percent Contrast	Contrast Sensitivity
1	0.93	.00	93	1.08
2	0.56	.02	56	1.79
3	0.44	.02	44	2.27
4	0.31	.02	31	3.23
5	0.15	.03	15	6.67
6	0.09	.01	9	11.11
7	0.03	.03	3	33.33

Procedure

The orangutans were randomly assigned to select a target, with Sekali trained to select vertical and Ramai trained to select horizontal lines. On each testing trial two gratings were displayed, one oriented vertically and one oriented horizontally, matched in SF and contrast. Left and right locations of the target stimulus were in a predetermined order that was randomized and limited to three successive trials at a location. A research assistant loaded the two stimuli onto the two podiums of the display unit so that the experimenter was blind to the location of the target stimulus. On each trial the experimenter removed a panel to reveal the stimuli to the orangutan, but the stimuli were out of view of the experimenter. Once the orangutan had made a selection by touching a podium with the dowel, the experimenter verified whether the orangutan had selected the target by leaning forward and peeking over the display unit to see the stimuli. If the target was correctly selected, the orangutan was reinforced immediately with either verbal

praise: “Good job” for Sekali or a whistle for Ramai. The orangutans also received a food reward: small pieces of fresh or dried fruit, nut, or candy. If the orangutan selected the comparison stimulus instead of the target, the experimenter tapped on the correct stimulus with a finger and said: “This one” for Sekali or remained silent for Ramai. The experimenter then closed the display unit and did not offer a food reward. Selection was defined as the first stimulus that the orangutan touched with the dowel. Any unclear selections, such as touching the space between the podiums, were recorded as incorrect trials.

The initial training stimulus was a highly visible grating (0.5 c/deg and Michelson contrast of 0.93). Early training consisted of up to 60 trials per day to maximize learning given the constraints of the zoo schedule. Discrimination testing began on the first day that the orangutan selected the target stimulus on 17 out of the first 20 trials. Discrimination testing consisted of 20 trials per day on three consecutive days. Once the orangutans reached the criterion of 17 out of 20 correct selections across three consecutive testing days, then this was followed by a generalization phase with gradually increasing SF and gradually decreasing contrast. The orangutans were acclimated to these stimuli slowly because the more difficult stimuli resulted in more errors, less reinforcement, and increased agitation in the orangutans. This phase continued three times a week for several months before our final threshold testing; access was limited due to the zoo schedule and training sessions were sometimes prevented for practical reasons.

For our final threshold measurements, we used the staircase method of stimulus presentation (Cornsweet, 1962; García-Pérez, 2001). The seven contrast levels served as the steps of the staircase. The staircase began at the highest contrast (easiest step) and progressed through the contrast values to the lowest contrast (most difficult step). At the start of each

staircase, a single trial was given at each contrast beginning at the easiest until the orangutan made the first error. Then we switched to a 2-down-1-up rule: the orangutan now had to complete two correct trials at each contrast step before progressing to the next more difficult contrast ("2 down"), and whenever an error occurred we immediately returned to the previous step ("1 up"). Simulations using this criterion track a threshold level of 71% correct responses (Garcia-Perez, 2001). Each change in direction in the staircase is referred to as a reversal. A staircase was continued until eight errors had been made, and thresholds were calculated by averaging stimulus values (log contrasts) at the last six reversals. On each of the three testing days, the orangutans completed four separate staircases, one for each of the four grating frequencies (2, 4, 10, and 15 c/deg). The order of presentation of staircases was counterbalanced across testing days. Thresholds were averaged over the three days for each spatial frequency and CS at that SF (1/threshold) was calculated.

A quality check with three human observers was completed to verify the validity of the apparatus and stimuli; this was done using the same apparatus and stimuli, under lighting that matched the stimulus luminance used at the zoo. However, due to practical circumstances this was carried out in a laboratory setting where ambient lighting could be controlled and adjusted to match measurements made at the zoo.

Results

Training results

Sekali reached the training criterion with the 0.5 c/deg stimuli after approximately six weeks of training three days per week. Ramai took much longer to learn the discrimination, meeting the criterion after 10 weeks. Interestingly, Ramai reached the criterion three training days after we switched her procedure from verbal feedback with a food reward, to a whistle-blast

with a food reward. A whistle was never used for Sekali. Individual differences in motivation and social behaviour were the reason for this change in procedure; we observed that Ramai was less motivated by social reinforcement, and easily distracted by a human voice and eye contact. In contrast, Sekali demonstrated high motivation in response to social reinforcement.

Threshold values produced by staircase procedure

A threshold was estimated from each staircase run by averaging the contrast values at the last six reversals of the staircase. Contrast sensitivity scores (reciprocal of threshold) for each orangutan on each test day at each test SF are shown in **Table 4.2**, along with their CS averaged across the three test sessions. CS was highest at 2 c/deg for both orangutans and declined gradually as SF increased. **Figure 4.2** shows sample staircase data for Sekali at the lowest SF tested (2 c/deg) and for Ramai at the highest SF (15 c/deg). These figures reveal two problems encountered using the staircase that led us to believe that the thresholds measured underestimate the orangutan's optimal performance, particularly at low SF. As can be seen in **Figure 4.2a**, despite extensive prior experience with these stimuli, some learning effect was evident with the staircase procedure in that more errors were made at the higher contrasts on the first run than on the later runs. This general pattern was displayed by both orangutans at the lower SF (2 and 4 c/deg) and by Sekali at the higher frequencies as well. Secondly, it is clear that at 2 c/deg Sekali shows a ceiling level of performance with most trials at the most difficult stimulus level. In the final session, after two errors she made 23 consecutive correct responses to this stimulus; and there were several instances of runs of six or more consecutive correct responses at the lowest contrast step at SF of both 2 and 4 c/deg. While not showing such a pronounced ceiling effect, Ramai also achieved runs of five consecutive correct responses for both of these lower SF. This indicates a serious limitation of the printed stimuli we used; the lowest contrast (0.03) we were

able to produce was equivalent to a CS of only 33, whereas CS values of over 150 (contrast < 0.007) have been reported for humans. Thus from the staircase data alone we are not able to make a good estimate of CS at low SF.

Table 4.2

Contrast Sensitivity Averaged Over The Last Six Reversals From Three Testing Sessions

	Testing day	2 c/deg	4 c/deg	10 c/deg	15 c/deg
Sekali					
	Day 1	19.25	17.67	2.31	2.90
	Day 2	13.52	19.25	11.30	2.44
	Day 3	33.33[a]	14.38	4.16	8.61
	Average CS	22.03	17.10	5.92	4.65
Ramai					
	Day 1	14.77	5.85	2.71	1.39
	Day 2	16.23	11.98	1.73	1.53
	Day 3	17.67	14.72	2.24[b]	1.44
	Average CS	16.23	10.85	2.23	1.45

[a]*On Day 3 Sekali selected the target stimulus at the lowest contrast at 2 c/deg for 23 sequential trials so the trial was concluded after two warm-up errors (40 trials total)*
[b]*On Day 3 Ramai only had four reversals despite eight errors due to a drop in affect*

At the highest SF tested (15 c/deg; see **Figure 4.2b**) Ramai's performance was close to chance, suggesting that we were able to approach the acuity limit with our available stimuli. Not apparent from the graph is the fact that approximately 50% of trials at the highest contrast (0.93) were errors but, as we were at the top of the contrast scale, the staircase could not go further up. Sekali showed poor performance on the first day she was tested with the higher frequency patterns, and improved although performance was quite variable thereafter.

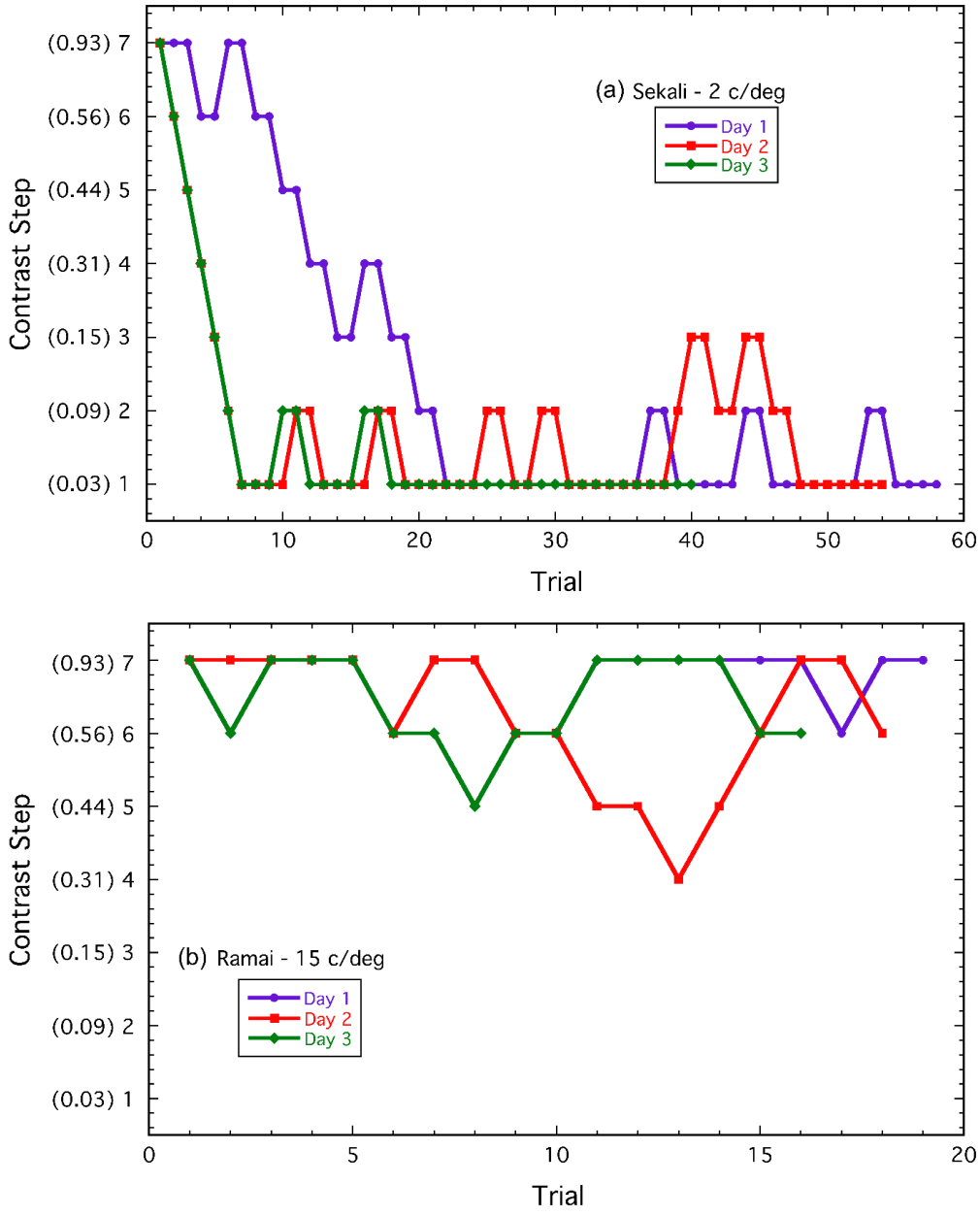

Figure 4.2. Examples of staircase progression for Sekali at 2 c/deg (a) and Ramai at 15 c/deg (b); trial number is plotted against contrast sensitivity step for three days. With successful performance, both orangutans progressed down the staircase from high contrast (0.93) to the lowest contrast (0.03) steps. Note that the contrast steps do not represent equal increments in contrast, and due to the number of trials the scales are not the same.

Thus, based on the staircase analysis alone, we can say only that the CSF of both orangutans peaked at 2 c/deg or below, and that at the high end, the orangutans were approaching or had reached the acuity limit (CS = 1) by 15 c/deg. Factors beyond our control precluded more extensive testing. Therefore, in order to optimize our threshold estimates, we have also used a second approach to analyzing the staircase data.

Although under ideal conditions adaptive procedures like the staircase track thresholds efficiently, they provide little information about performance at superthreshold stimulus values. In order to take advantage of all the data collected, we also looked at cumulative scores (% correct) on each contrast/SF combination tested. This allowed consideration of all trials (N = 835), rather than just the reversal trials (N = 144). In order to estimate thresholds from this data we plotted the percent correct scores against log contrast for each SF for each orangutan, fit these data using a Quick function (Quick, 1974) and defined the threshold as the interpolated 75% correct value.

Contrast sensitivity values (1/threshold) derived from the staircase (red) and Quick function (blue) thresholds are plotted against SF in **Figure 4.3**. The average of the staircases (red) is derived from **Table 4.2**. In order to obtain an estimate of the function that would relate CS to SF over the full SF range, we adapted the model used by Wilson and Giese (1977) to fit human data for sustained stimuli: $CSF = A * \omega * e^{-\omega/\sigma}$

Spatial frequency is denoted by ω. The function has two free parameters: A is a gain factor determining the overall height of the function and σ is the SF at which the function peaks. In **Figure 4.3**, the dashed red and blue lines are the best fits to the thresholds estimated from the staircase and Quick function analyses respectively for Sekali (**Figure 4.3a**) and Ramai **(Figure 4.3b**). For both orangutans, estimates of grating acuity (CS = 1) are very similar using the two

threshold estimate techniques (Sekali: 19.5 & 16.2 c/deg; Ramai: 15.0 & 13.5 c/deg). Although the Quick function measurements yielded higher CS at low SF, peak sensitivity was predicted in the same region (2.4 – 3.5 c/deg) for both orangutans and model fits. It should be noted that this model, which is based on human sustained data, has a low-frequency fall-off built into it. Based on our behavioural data alone, both orangutans showed greatest sensitivity at 2 c/deg, so we cannot rule out the possibility that the shape of the underlying function peaks at or even below 2 c/deg in this species. Further testing with lower contrast stimuli at these SF would have provided more information about the curve; however, this was the lowest contrast that we could produce with the printer and we would have faced parallel difficulties displaying reliable contrast on a screen.

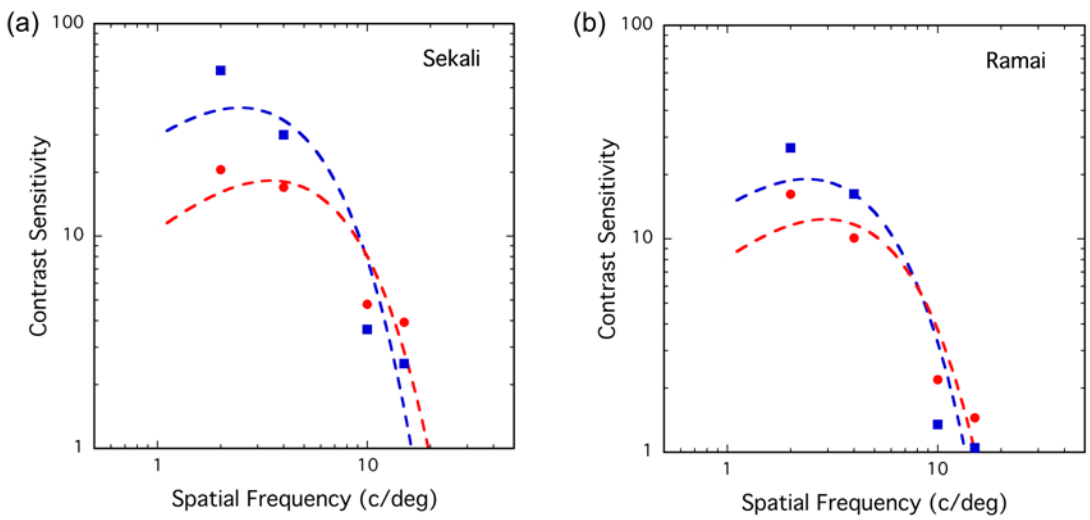

Figure 4.3. Contrast sensitivity function of the two orangutans: Sekali (a) and Ramai (b). The log scale of CS is plotted against log scale of spatial frequency (2, 4, 10, 15 c/deg). The red line indicates the CSF derived from the staircase, and the blue line shows CS from the percent correct Quick fit.

For the purpose of comparison, we used the same model to fit the CS data for four chimpanzees and one human published by Matsuno and Tomonaga (2006a; see **Figure 4.4a**); exact data values were generously provided to us by the authors. In their study, thresholds were measured over a range of five SF from 0.5 to 8 c/deg. As can be seen in **Figure 4.4a**, the chimpanzee and human functions are a very good fit to the data, and peak sensitivity falls between 1 and 2 c/deg for all chimpanzees and for the human tested under comparable conditions. In **Figure 4.4b** we compare those data to the CSF functions (Quick thresholds) for the orangutans shown in blue. Here we have combined the data of three chimpanzees with similar data to produce an "average chimpanzee function." The fourth chimpanzee (C3 in **Figure 4.4a**) showed lower CS, possibly due to an ocular problem that was detected later (*T. Matsuno personal communication Jan 28, 2016;* Kaneko, Sakai, Miyabe-Nishiwaki, & Tomonaga, 2013), so it was not included in this average. It is clear that while overall sensitivity was lower in the orangutans, peak sensitivity lies at the same SF and visual acuity, as estimated by extrapolating the function to CS = 1, is at least as high in the orangutans as in the chimpanzees in Matsuno and Tomonaga (2006a).

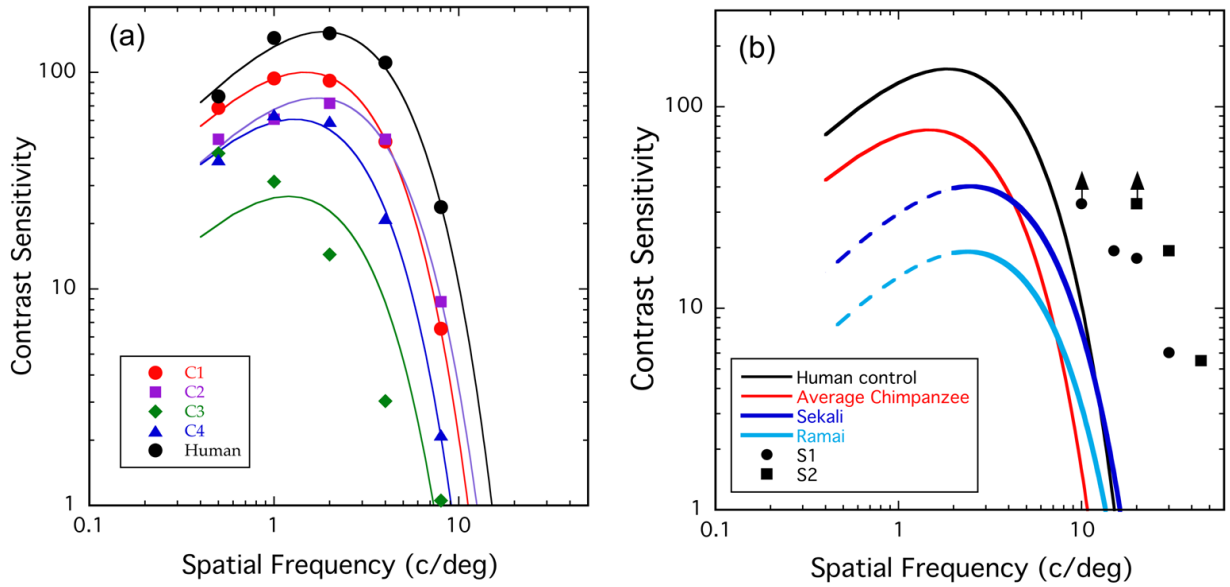

Figure 4.4. (a) CSF fits to the data of four chimpanzees and one human control generously provided by Matsuno and Tomonaga (2006a). Chimpanzee 3 was later found to have an arachnoid cyst in the visual area (Kaneko et al., 2013). (b) CSF for Sekali and Ramai fit as described in the text, shown here with the functions fit to the Matsuno & Tomonaga results for comparison. For Sekali and Ramai, solid lines are used for the portion of the curve derived with actual data and dashed lines for extrapolated data. Also shown are staircase-derived contrast thresholds for two human subjects tested with our procedures and stimuli. Data points with arrows indicate the highest SF at which their performance was 100% correct for our lowest contrast stimulus, indicating that their true threshold lies above the indicated point.

We also tested three human subjects (2 authors and 1 additional adult female). We used the same apparatus and stimuli as with the orangutans, illuminated by overhead lighting adjusted so that the stimulus luminance matched that of the zoo stimuli (20 cd/m^2). Procedures were identical to those reported above except food reinforcement was omitted. Two of the three humans performed perfectly at all SFs and contrasts at 57cm and the third made errors only at 15

c/deg and the lowest contrast. Because thresholds could not be assessed under these conditions, two subjects were also tested at 114 cm and at 171 cm, which increased the range of high SFs tested to include 20, 30 and 45 c/deg. Because the subjects had 100% correct performance for all SFs below 15 c/deg at all test distances, we could not estimate the location of the peak sensitivity or fit a meaningful function to the data. However, based only on thresholds at 20, 30 and 45 c/deg, which are plotted in **Figure 4.4b**, it was clear the cutoff (CS = 1) for one individual would fall between 30 and 45 c/deg whereas the other would fall above 45 c/deg. This confirms that our procedures produce comparable high SF contrast thresholds to those produced in more traditional human psychophysical setups (Campbell & Robson, 1968; De Valois et al., 1974).

Discussion

The CSF as a description of the spatial sensitivity of the visual system is characterized by its overall height, the position of its peak along the spatial frequency axis, and its cutoff frequency, the SF beyond which the stimulus pattern is not resolvable even at maximum contrast (CS = 1). In the present study, we have shown that the CSF of orangutans is generally similar to that of other species studied in terms of shape (Uhlrich et al., 1981), and its peak (2 – 3 c/deg) falls at the low end of the range reported for similar luminance conditions in primates (see **Appendix E**). However, overall sensitivity was – at least under our test conditions – considerably lower than that reported for diurnal haplorhines tested in laboratory conditions (**Appendix E**), and extrapolated cutoff spatial frequency (visual acuity) was found to be between 13 and 20 c/deg in the orangutans, again lower by a factor of three than the best estimates in humans and macaques (45 – 60 c/deg). It is possible that this indicates a marked divergence of orangutan spatial vision from that of other great apes, and given its very separate evolutionary history, its more arboreal lifestyle, and the extreme lack of existing documentation of the

anatomical and physiological properties of its visual system, this possibility cannot be ruled out. However, it seems more likely that the differences can be explained more simply in terms of aspects of the test conditions. In humans and macaques, a wide range of stimulus and subject variables have been shown to affect both the overall level of sensitivity and the location of the peak of the CSF (e.g., luminance: De Valois et al., 1974; stimulus size: Campbell & Robson, 1968; subject age: Arundale, 1978; Boothe et al., 1988). It is also possible that these two orangutans are not good representations of typical orangutan vision due to chance, or due to some aspect of their living conditions. The orangutans do not have access to outdoor areas, which is similar to studies of laboratory macaques; however, future studies should investigate vision of orangutans raised in natural environments.

Comparison to chimpanzees

The only prior CSF measurement in a non-human great ape is the study of chimpanzees reported by Matsuno and Tomonaga (2006a). They collected data at five spatial frequencies between 0.5 and 8 c/deg using the PEST procedure, an adaptive staircase that generally requires fewer trials to estimate thresholds than the staircase used in the present study (Taylor & Creelman, 1967). The function we used to fit our data also provided an excellent fit to the chimpanzee thresholds; the chimpanzees displayed greater sensitivity at the peak (average peak CS = 128) than the orangutans, but the location of the peak was lower in the chimpanzees (average peak = 1.3 c/deg vs 2.8 c/deg). Importantly, the extrapolated high frequency cut-offs in CS were also low, giving acuity estimates (9 –12 c/deg), which fall below those of the orangutans, and far below the acuity measures reported in two chimpanzees by Spence (1934) using diffraction gratings (approximately 35 and 60 c/deg in the luminance range tested here), and in one chimpanzee tested by Matsuzawa (1990) using a letter matching test (letter acuity =

1.5; equivalent to grating acuity of 45 c/deg). Surprisingly, the single human subject in the Matsuno and Tomonaga (2006a) study showed a similar pattern of unexpectedly low peak location (1.9 c/deg) and cutoff SF (15.1 c/deg) even though the CS value at the peak (155) was in the low-normal human range. In contrast, human participants in our study showed performance at higher spatial frequencies that was much better than that of the orangutan subjects and predicted cutoff SFs in the normal human range of 35 – 50 c/deg. This suggests that the height and position of the CSF in the Matsuno and Tomonaga (2006a) study may have been affected by some aspect of their stimuli impacting human and chimpanzees alike, whereas in our study, the low thresholds are more likely due to differences in either motivation or testing procedure for the orangutans. A likely candidate limitation in the chimpanzee study is the limited size of the Gabor pattern stimuli. A study of macaques (*Macaque nemestrina*) by Kiorpes and Kiper (1996) with small targets and short stimulus exposures produced very similar CSF functions to those reported in the chimpanzees and in orangutans in the present study, despite high luminance, and testing procedure otherwise identical to those used in earlier studies from this group.

Possible contributors to the lower CSF of the orangutan

At the lowest spatial frequency for which we gathered contrast thresholds (2 c/deg), our measurements undoubtedly underestimate the true abilities of the two orangutans because they both showed ceiling level performance at the lowest contrast stimulus we were able to produce, as did all of the human subjects tested in our apparatus. This was a serious limitation of our hard-copy stimuli as it allows us only to say with certainty that threshold contrast at 2 c/deg is considerably better than the lowest contrast we were able to present. However, at the higher frequencies, especially 10 and 15 c/deg, the range of stimulus contrasts available was adequate to track threshold performance using our staircase procedure, and when we incorporated all test

trials into our analysis to calculate 75% correct performance, thresholds changed very little at 10 and 15 cycles (see **Figure 4.3**). Overall luminance and stimulus size are not likely to account for the depressed performance as luminance was in the same range as those reported in **Appendix E**, and our stimuli were large and close to the orangutans. Viewing distance was quite constant as the orangutans always moved their eyes right up to the cage mesh. In view of our own observations and details provided in the reports of other studies (Cowey & Ellis, 1967; Spence & Fulton, 1936; Tigges, 1963), we speculate that a combination of the distracting conditions in the zoo, task difficulty, and fluctuating motivation levels in combination with limitations in the amount of data we were able to collect within and across test sessions together account for the thresholds we obtained. The orangutans were rewarded with pieces of preferred food; however, unlike many earlier primate studies (e.g., Cowey & Ellis, 1967), the orangutans were not food deprived. The orangutans were tested in their home enclosures so distractions included view of conspecifics and enrichment objects. Other reports of performance in orangutans reflect a similar lack of focus in a test context and poor performance on simple discriminations (Davis & Markowitz, 1978; Schrauf & Call, 2009) and on list learning (Swartz et al., 2007). Other studies of Ramai and Sekali along with other Toronto zoo orangutans have shown a similar pattern to slow discrimination acquisition and maintenance performance of well under 100% correct (Marsh et al., 2011), including studies on topics that we would expect to elicit more intrinsic interest such as picture recognition (Marsh & MacDonald, 2008). It would be interesting in light of the present results to filter complex stimuli used in cognitive studies using the high frequency attenuation our current results suggest: this might reveal the aspects of the patterns most salient to orangutans.

The task we used in our study (vertical vs horizontal orientation discrimination), which has been used in other acuity measures (Ordy & Samorajski, 1968; Treff, 1967; Veilleux & Kirk, 2009), provides better experimental control than the more common stripes versus homogeneous field, but it is more difficult for animals to learn and maintain. Whereas the orangutans were extensively over-trained on a range of spatial frequencies and contrasts after reaching our learning criterion, they nevertheless showed variable performance across days on the staircase threshold assessments, and made mistakes on early trials. The staircase itself may also have provoked frustration in the animals, as easy trials occurred only at the beginning of a test. Spence and Fulton (1936) commented that one of his chimpanzees hated to make errors and would have temper tantrums or stop responding when the task became at all difficult, and the other made careless errors throughout leading to a much flatter frequency-of-seeing curve. Tigges (1963) similarly reported temper tantrums in a young orangutan when transferred to a more difficult version of a grey versus yellow color discrimination. Unfortunately, by the time we became aware of some of the shortcomings of the staircase procedure as we had implemented it, we were not able to improve the protocol due to lack of continuing access to the orangutans as they were involved in new studies. If such a study were repeated, we would recommend changing the testing in the following ways: 1) set a much longer reversal criterion – for example test until 12 reversals had occurred and average only the last 8, 2) insert occasional much easier "reminder" trials into the staircase procedure to reduce frustration, and 3) run several additional days of staircase testing so that the first 1 – 2 days could be treated as practice and not included in final threshold calculations. Even with these changes, we doubt that thresholds in the orangutans would have been improved to the level reported in laboratory testing of other diurnal primates, as too many other factors can impact performance in the zoo setting.

Future questions and conclusions

The present study provides a first look at spatial vision in Sumatran orangutans. We hope that future studies will examine other visual abilities of orangutans, particularly visual motion and depth perception, as these are skills critical to arboreal survival. A comparison of CSF across primate species and ecological niches would also be a valuable next step. CSF has been measured in only a handful of primate species, the majority of which are habitat generalists, making ecological inferences difficult (**Appendix E**). Future research could compare CSF across diverse primate species, in particular across diurnal/nocturnal niches, phylogenetic branches, and habitats. Comparisons across mammals, birds, and fish have found a similar shape of CSF despite differences in acuity and contrast sensitivity (Uhlrich et al., 1981), with birds showing high acuity but low contrast sensitivity (Ghim & Hodos, 2006). It would be interesting to examine whether this trade-off is observed in primates. In particular, it would be useful to compare the CSF shape, acuity, and contrast sensitivity for species specialized to habitats at extremes of light, (e.g., a mid-canopy tropical rainforest species that largely encounters filtered light versus a species that lives exclusively in bright open savanna). Our results suggest that the orangutan may not have as sensitive spatial vision as expected from considerations of eye size, phylogeny, and niche (Veilleux & Kirk, 2014). However, an answer to the question of whether the orangutan spatial vision is truly anomalous will await further behavioural studies, and anatomical assessment of the Nyquist limit of the foveal retinal mosaic and the pattern of connections between foveal cones and midget ganglion cells, the two main anatomical determinants of human visual acuity (Rossi & Roorda, 2010; Williams, 1988). In the meantime, our findings provide a valuable picture of the range of visual stimuli that one can be confident will be effective as experimental stimuli and as environmental enrichment for the orangutan.

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CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

Orangutan photo preferences

The first aim of this dissertation was to design a method of measuring photo preferences and to investigate some orangutan photo preferences. This was accomplished in Chapter 2: a method of presenting two images on two laptops was developed, and preference was found for images of orangutans over humans, familiar orangutans over unfamiliar orangutans, and some age/sex characteristics of conspecifics. This approach confirmed spontaneous differentiation of these categories of photos and supported the view that untrained looking behaviour is similar across primates. This is evidence that training was not required for orangutans to perceive some of the content of the photographs. Some spontaneous visual preferences could be products of evolved looking behaviour; Fujita and Watanabe (1995) cited evolutionary explanations for spontaneous visual preferences in several macaque species that preferred pictures of their own species. Learning may also influence preference: rhesus macaques initially only showed novelty preference for pictures of their own species, but with exposure to pictures of new animals, they shifted to a novelty preference in pictures of new animal species (Humphrey, 1974).

To build on Chapter 2, we designed a touchscreen apparatus for studies in Chapter 3. This could potentially give a better measure of preference, and a larger sample size due to automatized coding. The touchscreen data showed preferences, with orangutans preferring images that featured an animal over images that did not. However, again we did not find large differences in preference, or sufficient sensitivity to investigate preferences beyond broad categories. The orangutans did not use the touchscreen for prolonged sessions, so we did not obtain large amounts of data. We developed Chapter 3 into an assessment of methodology,

focusing on comparing the passive looking time apparatus and the active touchscreen, assessing participation and preference across these paradigms.

The testing environment, social context, and prior experience of the subjects are important factors to consider in designing and interpreting a research project. In Chapter 2 we found that orangutans participated more when both screens featured faces of conspecifics, a high interest category, which is evidence that motivation was a factor in participation levels for the different studies. I predicted high participation and motivation in general, based on my prior experience with great apes. As part of a research pilot, I had observed play behaviour in rehabilitant orangutans at the Samboja Lestari Orangutan Rehabilitation Project in East Indonesian Borneo. Young orangutans in socialization cages had extreme interest in human artifacts, for example, playing with a discarded rice sack for hours or a stolen hat until it was annihilated. The rehabilitant orangutans had low access to human artifacts; such objects are deliberately limited to minimize orientation to humans and improve success when released back into the wild. These individuals would have likely engaged eagerly with the apparatus in Chapter 2 and 3. I had also worked with cross-fostered encultured chimpanzees during an internship at Central Washington University. These sign-language trained chimpanzees maintained high interest in photographs and television. One of my inspirations for the preference project was observing these chimpanzees flipping through the pages of magazines, looking at pictures due to intrinsic interest without reinforcement. The low participation levels by these zoo orangutans was surprising given these experiences, but informative: it underscored the importance of rearing history, species, research context, and individual differences.

One important aspect of experience and context is the prior and concurrent research conducted with these orangutans (see **Appendix A** for their research history). In assessing prior

and concurrent experimental history, the most concerning overlap would be any studies that reinforced the same behaviour, specifically touching the touchscreen. Of the three orangutans who participated in our touchscreen study (Ch 4, Study 2), Budi had never used a touchscreen but the other two had been reinforced for touching a touchscreen image of orangutans, gorillas, shapes, and objects (Marsh, Adams, Floyd, & MacDonald, 2012; Marsh & MacDonald, 2008; Marsh, Spetch, & MacDonald, 2011). Both animal and non-animal categories had been reinforced, potentially cancelling each other out, and preference for animal stimuli was observed in all three orangutans despite different experimental histories. These prior studies with the same orangutans differed in procedure: the screen displayed images to be selected, whereas in our research the screen was blank until touched.

Although looking behaviour had not been reinforced in these orangutans, the prior studies rewarding photo behaviour could have biased the looking time study due to two processes: habituation and associative learning. If a category of photos was viewed extensively in prior research, then there is a possibility that the orangutans would not look as long at images from this category in subsequent studies due to habituation, i.e., preference for the novelty of the comparison stimuli. Associative learning from prior research could also potentially influence looking time behaviour. If an orangutan had previously been reinforced for selecting images from a particular category, then viewing images from this category could result in positive affect associated with the food reward, creating a bias for these images. If this were the case, we would expect it to influence results in the opposite direction from habituation. Both animal and non-animal stimuli have been reinforced for the same orangutans, so it is difficult to make any conclusions about prior reward history for Chapter 3.

Prior research is also of interest for the studies in Chapter 2. The majority of recent research did not feature images relevant to the comparisons, i.e. they did not include photographs at all, or featured images of food. However, a study with data collected in 2007 rewarded Ramai and Molek for selecting pictures of orangutans over other primates, and rewarded Jahe and Sekali for selecting images of gorillas over other primates (Marsh & MacDonald, 2008). This could have biased the Ramai and Molek to prefer images of orangutans in the orangutans versus humans comparison. However, all subjects showed preference for orangutans, even experimentally naïve Budi, and Ramai and Molek did not appear to have a larger magnitude of preference for orangutans than the other orangutans. Another study, with data collected in 1999, reinforced Jahe and Molek for selecting images of orangutans. It is unlikely that the orangutans maintained this training over 10 years and with multiple intervening studies. Molek participated in several studies by Vonk with data collected in 1999-2000 featuring animals and objects. Molek did not show particularly high distinctions in preferences, so these studies may not have influenced his preferences. However, they may explain Molek's high participation rate; he may have increased interest in photographs due to his research participation history.

It is also important to evaluate the possibility of inter-test effects within the current research, because the same orangutans participated in multiples studies. There was not a risk of associative learning because there was no food reinforcement in the preference studies and the rewarded CSF data were collected last. However, potential habituation to stimuli across the preference studies had the potential to bias preferences. The possibility for inter-test effects due to habituation of repeated categories of images was possible between Study 1 and 2 of Chapter 2, as both featured unfamiliar orangutans, which were compared to unfamiliar humans and familiar orangutans respectively. Habituation in this case seems unlikely as the unfamiliar orangutans in

in the two studies differed, and the category of "unfamiliar orangutans" is relatively heterogeneous. Study 2 and 3 both featured familiar orangutans, so it is possible that the orangutans habituated to the featured familiar orangutans in Study 2. This is mitigated because half of the stimuli for Study 2 featured Jahe, a juvenile female who was removed from the stimuli in Study 3 because she was at an intermediate age, neither infant nor adult. As such, only a minority of the familiar orangutans overlapped from Study 2 and 3.

Although it is unlikely that prior research influenced preference, it would not refute our findings. Preferences are mediated by experience, so prior research would be one of the many experiences contributing to preference. For example, if orangutans showed a looking preference for images of orangutans, this may be the result of both inborn tendencies as well as associative learning from positive interactions with other orangutans, playing with mirrors, any pictures displayed by the zookeepers, decorations, books and videos as part of their enrichment, as well as pictures in prior research. Working with zoo orangutans involves a rich history of interactions that cannot be explicitly accounted for, unlike the controlled picture exposure of laboratory subjects. Although this introduces an unknown history of picture exposure, it also makes zoo orangutans' picture experiences much more similar to those of most humans, who experience pervasive picture exposure from birth, often in contexts that may be characterised as leading to associative learning. For example, human caregivers show infants picture books, pointing at images while providing social reinforcement such as cuddling and smiling.

Orangutan spatial vision

The second aim of this dissertation was to verify whether orangutans have spatial vision similar to humans. Researchers have assumed that orangutan visual ability is similar if not identical to humans so measuring the orangutan CSF would complete a missing step. We

conducted our preference studies under this same assumption, that orangutan vision is similar to humans. The CSF study was inspired by the fact that we had obtained variable outcomes in our preference studies, and the realization that there were scant reports of orangutan visual abilities. Our findings were surprising: the orangutans we tested showed lower sensitivity than humans and macaques. There could be variability across nonhuman primate vision due to different selective pressures and habitat. But, as discussed in Chapter 4, we propose that the differences we found were due to testing conditions: distraction, low motivation, and practical limits to the data that we could collect. Measurement of orangutan vision in a zoo is not equivalent to that of macaques in a laboratory, or humans in clinical tests.

It is possible that orangutans behave differently in a testing situation from comparison species. Orangutans have been slow to learn simple associations, with frequent errors even on an overlearned task (Davis & Markowitz, 1978; Marsh & MacDonald, 2008; Marsh et al., 2011; Rumbaugh & Rice, 1962; Schrauf & Call, 2009; Swartz, Himmanen, & Shumaker, 2007). Perhaps orangutans are resistant to training and conditioning because they adhere to an incorrect strategy thus preventing learning by simple associations. Marsh and colleagues (2013) found that younger children outperformed older children on a simple task, as older children had a tendency to “overthink” and described using complicated incorrect strategies. Complex cognition therefore has the potential to confound a simple task and interfere with conditioning. Further limitations to orangutan research are small sample sizes due to small captive populations, and consequently less ability on the part of the researcher to exclude individuals that do not quickly acquire the task.

The slow associations in our study may also be an outcome of testing outside a laboratory environment and without food deprivation. For example, Rumbaugh and Rice (1962) found very

slow learning in young zoo-housed great apes' discrimination of red circle and red triangle wooden blocks. An orangutan required 280 trials, a gorilla 139, and a chimpanzee 273 to reach a criterion of 20 correct responses within 25 consecutive trials (80%). However, this performance was not maintained, and maximum performance for this relatively simple task was below 75% correct. The zoo environment may be more enriching in terms of toys, social contact, play areas, and varied unrestricted diet. This context may decrease motivation to participate in studies compared to a typical laboratory environment with its fewer competing interests. Research in laboratories may also have a separate testing enclosure that removes distraction from toys and social partners. Our subject orangutans also did not have an altered diet for testing, they continued a diverse diet of fruit and vegetables, chow designed for captive primates, and other items such as nuts. In comparison, laboratory primate research has used food deprivation to increase motivation. Of the seven articles that we cited to compare nonhuman primate CSF (Chapter 4, **Table 3.1**), five did not mention whether there was food deprivation or not (Boothe, Kiorpes, Williams, & Teller, 1988; De Valois, Morgan, & Snodderly, 1974; Jacobs, 1977; Matsuno & Tomonaga, 2006a; Williams, Boothe, Kiorpes, & Teller, 1981). Merigan (1976) tested squirrel monkey vision before feedings to increase motivation with hunger, and Langston, Casagrande, and Fox (1986) restricted the diet of galagos so that they were 85% of their *ab libitum* weight when tested. Further, if the usual diet is homogenous, for example, monkey chow, then motivation for high-value reinforcement may be similar to that induced by food deprivation. Cowey and Ellis (1967) found that squirrel monkey "apathy toward the standard diet produced a self-imposed deprivation" (p.82) so that they performed for reward as if deprived.

If orangutans actually do have the low sensitivity reported in Chapter 4, an important step would be to assess if orangutan spatial vision is sufficient to consider them capable of perceiving

stimuli in experiments. For example, if orangutan spatial vision is very poor it could be a confounding variable in studies using visual stimuli. Future research could filter stimuli to account for orangutan CSF, as images have been filtered to simulate human infant vision (Vázquez, Sossa, & Garro, 2010). Our extrapolated spatial frequency cutoff was 13-20 c/deg, equivalent to at least 13 pairs of white and black lines printed on your thumbnail held out at arm's length. This is a very fine distinction, so it may not have impaired use of photographs in Chapter 2 and 3. This is supported by the numerous studies showing successful use of photographs by orangutans (e.g., Chapter 2; Chapter 3; Marsh & MacDonald, 2008; Vonk & MacDonald, 2004). Further, Chapter 4 analysis showed chimpanzee CSF was even less sensitive in an analysis of data from Matsuno and Tomonaga (2006a), and chimpanzees have also demonstrated successful photo use (e.g., Matsuzawa, 2006; Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005; Tanaka, 2007; Vonk & Vedder, 2013). However, the frequent successful use of photographs may be evidence that measurement in Chapter 4 underestimated orangutan CSF, in our estimate due to motivation. Chapter 2 reports significant preferences between photographs that were relatively well balanced in characteristics such as colour and level of detail, for example comparisons of familiar and unfamiliar orangutans. As such, the preferences in Chapter 2 are a good indication that the orangutans are able to perceive at least some important aspects of an image without training.

The importance of testing context

Our preference and spatial vision outcomes showed orangutans to be different from other primates, but upon further reading, perhaps chimpanzees show similar difficulty in measuring vision and variability in preferences. As discussed in Chapter 2, chimpanzee research shows more complex patterns of preference (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013;

Myowa-Yamakoshi et al., 2005) than studies of macaque preferences (Fujita & Watanabe, 1995; Parr, 2011). Chimpanzees did not show preference for infants (Kawaguchi & Tomonaga, 2017), which is similar to our findings in Chapter 2 but differs from macaques' preference for infants (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012; Gerald, Waitt, & Maestripieri, 2006).

Studies of chimpanzee vision are limited, which is surprising given the availability of laboratory chimpanzees over the last century. Spence (1934) measured chimpanzee acuity, and although it appears that this study was replicated (Grether 1941; Prestrude 1970; Spence & Fulton, 1936), in fact these studies all simply re-examine Spence's original data on two chimpanzees. The only other study of chimpanzee acuity was conducted using a modified Snellen test (Matsuzawa, 1990) with "Ai", a chimpanzee whose unique relationship with the experimenter and testing environment may have allowed for better communication and better motivation and therefore better data.

In fact, the majority of recent reports of chimpanzee vision were conducted at the Kyoto Primate Research Institute which places strong emphasis on relationships of chimpanzees and researchers (Matsuzawa, 2006; Russon & Adams, 2008). Studies of acuity (Matsuzawa, 1990), color naming (Matsuzawa, 1985), CSF (Matsuno & Tomonaga, 2006a), temporal vision (Matsuno & Tomonaga, 2008), and motion detection (Matsuno & Tomonaga, 2006b) may have been successful due to this emphasis on relationships, testing environment, and corresponding motivation. This lends support to the idea that our results for vision estimates may be low due to motivation and testing context. Perhaps other research on great ape CSF has been attempted, found low sensitivity due to low motivation, and was not published, hence the scarcity of published reports of great ape vision. Managing motivation is important; earlier vision studies mention temper tantrums and emotional conflict which could confound measurement in

chimpanzees (Spence & Fulton,1936) and orangutans (Tigges, 1963). It makes sense that our behavioural measures of vision may be lower than expected; Caves, Brandley, and Johnsen (2018) explain that anatomical estimates provide theoretical upper limits of visual abilities such as acuity, while behavioural measurements typically show lower ability and are more realistic as they are subject to external conditions.

To investigate orangutan patterns of motivation and participation, a follow-up study could investigate simple task performance and associative learning to establish acquisition rates to discriminate stimuli for food rewards, as well as a baseline of correct responses for an overlearned simple task. These values could be factored into comparison with results obtained with laboratory macaques. Factors influencing success and motivation could be manipulated and assessed to give context to our data and other orangutan research that appears to show lower performance on simple tasks (Davis & Markowitz, 1978; Marsh et al., 2011; Marsh & MacDonald, 2008; Schrauf & Call, 2009; Swartz et al., 2007). Motivation versus a cognitive confound such as adherence to an incorrect strategy could be compared. Perhaps a bias such as expectation of food reward due to prior research experience, and resulting frustration, could be an intervening variable.

Conclusions

These studies of perception reveal important information about orangutans. Our findings serve as a caution against assuming that primates have identical perceptual abilities to humans, and that primate research findings will be similar across species, especially across macaques and great apes. Assuming similarity to humans can result in bias in our setup of apparatus and experimental design (MacDonald & Ritvo, 2016; Ritvo & Allison, 2014). Despite our lower than expected participation, there were clear advantages to using a spontaneous paradigm to measure

preferences, so we hope that future research will continue to build on these methods. Rewarded studies can elicit participation even if the stimuli are anthropocentric, artificial, or do not have features that subjects would attend to in their captive lives or would have been exposed to throughout their evolutionary history. In the case of a spontaneous paradigm, orangutans would not participate if they were not interested in the stimuli, so the apparatus functions as a filter to relevant stimuli and topics. Both spontaneous and rewarded studies can therefore contribute to research: with more specific hypotheses tested with rewarded paradigms, and the general results verified with a spontaneous method to remove the risk of training effects and to see behaviour in a more ecologically valid context. The variability we saw across subjects is a reminder to assess subjects' motivation, as a touchscreen might lead to large amounts of valuable data for one subject but no data or even aggressive interactions in others. Choice of an active or passive experimental apparatus should take into account the context, species, experimental histories, and social characteristics and individual differences of the subjects.

The goal of this dissertation was to measure orangutan vision and preferences to see if orangutans see as we do. Although vision and preference seem like simple elements to measure, the surprising result was how complex our data were. Orangutans did not show the same results as macaques nor as humans. However, the similarity was that orangutans, like humans, see with varied levels of attention and motivation, with influence from prior experience and context, with potential inborn tendencies and individual differences. It may be that orangutans show too much variability to expect simple outcomes, and their perception and looking behaviour are as varied and subject to context as our own.

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APPENDICES

Appendix A: Prior and Concurrent Research with the Orangutans

	Prior/concurrent research		Chapter 2	Chapter 3 Animal versus Non-animal			Chapter 4
	Animal images(S+)	No animals	Orang: Human, Familiar: Un Adult: Infant Male: Female	Looking-time	Touchscreen	Flashcards	CSF
Data collected	2004-2007 *before 2000*	2004-2011	2008	2008	2010/11	2010/11	2012
Jingga	Naïve	R10	A>I, M>F			A>Non	
Kembali	Naïve	R10	A>I, M<F	A>Non		A>Non	
Budi	Naïve	MM12, MM11, R10, M12	O>H F>UN**, A>I, M>F	A>Non	A>Non	A>Non	
Jahe	MM08(Gorilla) *VM04(Orang)*	MSM11, MM12, MAFM12, R10, M12	O>H**, F>UN***, A>I**, M>F*	A>Non	Moved to another zoo		
Sekali	MM08(Gorilla)	MSM11, MM11, MAFM12, R10, M12			A>Non	A>Non	CSF
Ramai	MM08(Orang)	MSM11, MM12, MM11, MAFM12, R10, M12	O>H* F>UN A>I, M>F**		A>Non	A>Non	CSF
Puppe	*VM04(Orang)*			A>Non		A>Non	
Molek	MM08(Orang) *V02,VM04, V13, VH14, X*	MSM11, R10, M12 *V03, V14*	O>H F>UN A>I, M>F	A>Non	Deceased		
Dinding	*VM04(Orang),VH14*	*V03*		Deceased			

*p<.05, **p<.01, ***p<.001, "<"indicates direction of mean for non-significant findings, which is included when between-subject comparison was significant and because only 1 of 20 comparisons had a higher mean in the opposite direction

Data collected in or before year 2000

X Spent time at Yerkes laboratory, early experimental history is unknown.

V02 Vonk, J. (2002). Can orangutans and gorillas acquire concepts for social relationships? *International Journal of Comparative Psychology*, *15*(4).

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V13 Vonk, J. (2013). Matching based on biological categories in Orangutans (*Pongo abelii*) and a Gorilla (*Gorilla gorilla gorilla*). *PeerJ*, *1*, e158.

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Data collected 2001-2007

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Data collected concurrently

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Appendix B: Overview of Visual Preference Research in Primates

Author	(N) Species	Food Reward	Method	Active/ Passive	General topic	Preference found for stimuli featuring
Anderson et. al., 2005	*6 Cebus apella, 4 Saimiri sciureus*	No/yes	Cards, touchscreen	Active	Faces, patterns	Regular/symmetrical stimuli, mixed result on face preference
Bard et al., 1995	*13 infant Pan troglodytes*	No	Looking-time	Passive	Pattern/grating	Teller acuity cards, grating over matched grey
Bloomsmith & Lambeth, 2000	*10 Pan troglodytes*	No	Looking-time	Passive	Animal vs non	Chimp & human>blank screen, human=Chimp
Breaux et al., 2012	*2 Pan troglodytes*	*inter-trial	Button	Active	Animal vs non	Chimp body parts > objects, no preference for characteristics of sexual body parts
Cacchione & Krist, 2004	*10 Pan troglodytes*	No	Looking-time	Passive	Impossible	Impossible object relations>possible
Demaria & Thierry, 1988	*11 Macaca arctoides*	No	Looking-time	Passive	Age/sex, species vs species	Infants>adults, own species, felids>other animals, conspicuous eyes>non
Dufour et al., 2006	*5 Macaca tonkeana, 5 Cebus apella, 9 human*	*juice	Looking-time	Passive	Faces	Novel vs previously viewed faces
Fantz 1958	*Pan troglodytes*	No	Looking-time	Passive	Pattern/grating	Visual abilities measured
Fantz 1965	*100+ human infants*	No	Looking-time	Passive	Faces, pattern/grating	Patterns, face-like stimuli
Fujita & Matsuzawa, 1986	*1 Pan troglodytes*	No	Button	Active	Animal vs non	Humans > scenery
Fujita 1993	*7 Macaca fuscata, 5 Macaca mulatta*	No	Button	Active	Species vs species	Own species> despite raised with other species, not when young
Fujita & Watanabe, 1995	*22 Macaque sp.*	No	Looking-time	Passive	Species vs species	4 of 5 preferred own species, Brunnescens didn't and is island species
Gerald et al., 2006	*12 Macaca mulatta*	No	Looking-time	Passive	Age/sex	Infants>adults, but not prefer pink baby face
Guo et al., 2009	*3 Macaca mulatta, 17 Ccanis familaris, 19 human infant, 19 human adult*	No	Looking-time	Passive	Other	Perceptual bias to left side of face in photo
Hanazuka et al., 2012	*1 Pongo pygmaeus*	No	Looking-time	Passive	Animal vs non	Mammals with four legs > inanimate objects
Hanazuka et al., 2013	*3 Pongo pygmaeus*	No	Looking-time	Passive	Familiarity	Current familiar conspecifics < unfamiliar, familiar from 10 years ago> unfamiliar
Hopper et al., 2018	*1 Gorilla gorilla*	Yes	Touchscreen	Active	Other	Touchscreen choices of food matched manual food choices
Humphrey & Keeble, 1974	*5 Macaca mulatta*	Yes	Button	Active	Other	Frightening stimuli
Humphrey 1972	*2 Macaca mulatta*	*inter-trial	Button	Active	Animal vs non	Animals (men/monkeys/other animals) > non (flowers/abstract paintings/food)
Humphrey 1974	*6 Macaca mulatta*	Yes	Button	Active	Species vs species	Novel own species > non, novel unfamiliar species=non but mediated by experience
Kano & Tomonaga, 2009	*6 Pan troglodytes, 21 human*	Yes	Eye tracker-Looking-time	Passive	Faces	Faces > other parts of photo
Lacreuse et al., 2007	*4 Macaca mulatta*	*inter-trial	Button	Active	Age/sex	Pre-ovulatory cycle male > female, faces

Marsh & MacDonald, 2008	*4 Pongo abelii*	***not a preference study, analysis of error trials				Striking visual features, opposite sex
Murai et al., 2005	*3 Pan troglodytes*	***not a preference study, analysis of error trials				Mammals >vehicles/furniture
Myowa-Yamakoshi & Tomonaga, 2001	*1 infant Hylobates agilis*	No	Head turn/tracking	Passive	Faces, familiarity	Face>non, human caregiver >human stranger
Myowa-Yamakoshi et al., 2005	*3 infant Pan troglodytes*	No	Head turn/tracking	Passive	Familiarity	Mother>comparison (at 4-8 weeks, not other ages), familiar human=unfamiliar
Neiworth et al., 2007	*12 Saguinus oedipus, 20 human*	No	Looking-time	Passive	Faces	Novel face> non but not at certain orientations/inversion
Ritvo & MacDonald, 2016	*3 Pongo abelii*	Yes	Touchscreen	Active	Other	Silence>music
Santos & Hauser, 2002	*23 Macaca mulatta*	No	Looking-time	Passive	Impossible	Impossible event video > non
Sato et al., 2012	*11 Macaca fuscata, 10 Cercopithecus campbelli*	No	Looking-time	Passive	Age/sex	Infants>adults
Tanaka 2003	*5 Pan troglodytes*	Yes	Touchscreen	Active	Species vs species	Human>chimp, chimp>other primate*-complex
Tanaka 2007	*3 young, 8 adult Pan troglodytes*	Yes	Touchscreen	unclear	Species vs species	Adults human>chimp, Young: no pref (2/3) or human<chimp (1/3)
Teller et al., 1974	*7(+) human infants*	No	Looking-time	Passive	Pattern/grating	Grating>homogeneous grey (acuity)
Turati et al., 2005	*16 human infants*	No	Eye tracker-Looking-time	Passive	Face	Faces, mechanism of faces through manipulated stimuli
Vonk & Vedder, 2013	*1 Pan troglodytes*	Yes	Touchscreen	Active	Species vs species	Human sex > chimp sex, human aggression= chimp aggression, eyes>genitalia
Waitt & Little, 2006	*13 Macaca mulatta*	No	Looking-time	Passive	Face	Symmetrical macaque face>asymmetrical
Waitt et al., 2007	*12 Macaca mulatta*	No	Looking-time	Passive	Age/sex	Young nulliparous females look longer at infants than older multiparous

Note. Looking-time is used extensively in cases that are similar to preference studies, for example, violation of expectation tasks and some vision assessments. The above table includes a sample of these, as cited in the manuscript.

Appendix C: Samples of Stimuli for Chapter 2

Chapter 2, Study 1: Orangutans versus Humans

Orangutans		Humans	
a)	b)	c)	d)

Chapter 2, Study 2: Familiar versus Unfamiliar Orangutans

Familiar		Unfamiliar	
e)	f)	g)	h)

Chapter 2, Study 3: Age/Sex Preferences for Familiar orangutans

Infant

i) j)

Adult female

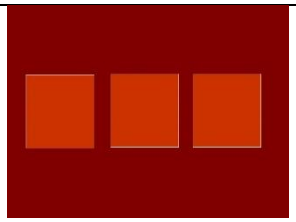
k) l)

Adult male

m) n)

Note. Image credits: a) Sumatran Orangutan by Anthony CC BY-ND 2.0; b) Young OrangUtan by Michaël Catanzariti CC BY-SA 3.0; c) Photo of Woman Planting by Bruce Mars, share without attribution; d) Small Child Arms Raised by Melanie, Meromex CC0 Public Domain; (g, h, j, k, m) Laura Adams; (e, f, i, l, n) Bill Longo with permission. We were unable to evaluate copyright for some photos used in the original stimuli, so images a-d are matched equivalent images.

Appendix D: Samples of Stimuli for Chapter 3

Animal Stimuli	Non-Animal Stimuli
a)	b)
c)	d)
e)	f) 
g)	h)
i)	j)
k)	l)

Note. Image credits: a) Canis lupus dingo 2 by Sam Fraser-Smith CC BY 2.0; b) Andreas Mikkelsen by Tiago J. G. Fernandes Portimão CC BY 2.0; c) Giraffe Standing by Miroslav Duchacek CC BY-SA 3.0; d) Swatches of carpet by Quadell CC BY-SA 3.0; e) Speedsuit by Chris Hunkeler, CC BY-SA 2.0; images f-l) Laura Adams. We were unable to evaluate copyright for some photos used in the original stimuli, so images a-d are matched equivalent images.

Appendix E: The Contrast Sensitivity Function in Primates

Authors	Species (N, age); [Human comparison]	Activity	Method	Luminance	Peak SF; CS [Human]	Extrapolated SF cutoff (CS = 1)
Langston et al., 1986	Galago *Otolemur crassicaudatus* (*N* = 2, adult)	Nocturnal	MOCS	22 cd/m²	1c/deg; 100	2.6 & 4.4 c/deg
Jacobs, 1977	Owl monkey *Aotus trivirgatus* (*N* = 2, adult); [H (*N* = 1, adult)]	Nocturnal	MOCS	11.4 cd/m²	1.5 – 2 c/deg; ≤100	≤10 c/deg
Merigan, 1976	Squirrel monkey *Saimiri sciureus* (*N* = 3, adult); [H (*N* = 2, adult)]	Diurnal	MOCS	3 cd/m²	2 – 5 c/deg; 95 - 120; [H: 200]	17 – 35 c/deg [H: 35 c/deg]
De Valois et al., 1974	Macaque *nemestrina; fasciculari* (*N* = 2, 1, adolescent); [H (*N* = 5, 15 – 25 years)]	Diurnal	MOCS	17 cd/m²	3 – 5 c/deg; 100; [H: 200]	40 – 50 c/deg
Williams et al., 1981	Macaque *nemestrina* (*N* = 4, 5 – 18 months); [H (*N* = 2, adult)]	Diurnal	MOCS	27 cd/m²	3 – 6 c/deg; 150; [H: 300]	40 – 50 c/deg
Boothe et al., 1988	Macaque *nemestrina* (*N* = 7, 1 – 12 months)	Diurnal	MOCS	27 cd/m²	3 – 6 c/deg; 100 (1 year) *variable	30 – 50 c/deg (1 year)
Campbell & Robson, 1968	Human study (*N* = 2) [adult]	Diurnal	Method of adjustment	500 cd/m², & 0.5 cd/m²	4 c/deg; 300+	~45 c/deg
Matsuno & Tomonaga, 2006a	Chimpanzee *Pan troglodytes* (*N* = 4, 21 – 28 years); [H (*N* = 1, adult?)]	Diurnal	PEST (1-up-1-down)	30 cd/m²	1 – 2 c/deg; ≤100	not specified
Current article	Orangutan *Pongo abelii* (*N* = 2, 20, 26 yr); [H (*N* = 3, adult)]	Diurnal	Staircase (2-down-1-up)	19 – 22 cd/m²	2 – 3 c/deg;	13 – 20 c/deg; [H: 30 – 45+ c/deg]

Note. Abbreviations: Human – H, Method of Constant Stimuli – MOCS. Human and macaque citations are representative of the studies focused on normal human and macaque CSF; normal control CSFs are also reported in numerous clinical studies.