

PhD thesis

**RECOGNITION OF INFANT FACES
IN GREAT APES**



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ACKNOWLEDGEMENT

First of all, I'd like to thank two great supervisors, Dr. Tomonaga and Dr. Adachi. Without their help I could not persuade my PhD. Under Dr. Tomonaga's supervision, we conducted more than three times as many experiments as I include in this thesis. It was an amazing time for me to explore chimpanzees cognition having him as supervisor. I have learned a lot from him. Dr. Adachi is always supportive and gives me constructive suggestions. I appreciate his academic guidance.

I also thank all chimpanzees who directly (as participants) or indirectly support my PhD work. I am grateful to past and present lab members, Ms. Etsuko Ichino, Ms. Akemi Hirakuri, Ms. Tomoko Takashima, Drs. Chloe Gonseth, Duncan Willson, Jie Gao, Cécile Sarabian, Fumito Kawakami, Mr. Hiroya Takiyama, Mr. André Gonçalves, Ms. Shenwen Xu, Mr. Ayumu Santa, Ms. Mikuho Yokoyama, Ms. Akiho Muramatsu for their assistance of my experiments.

I thank other section members, Drs. Tetsuro Matsuzawa, Misato Hayashi, Yuko Hattori, Makiko Uchikoshi, Ms. Yoko Ohyabu for their kind support including helpful comments. I thank the staff at the Center for Human Evolution Modelling Research for their daily care of the chimpanzees.

I appreciate the five reviewing committee members, Drs. Ikuma Adachi, Yuko Hattori, Hiroki Koda, Fumihiro Kano and Shinya Yamamoto.

I also thank co-authors and anyone who helped my experiment, including Drs. Satoshi Hirata, Fumihiro Kano, Naruki Morimura, Koyo Nakamura, Ms. Hanlin Yeow, Mr. James Brook, Mr. Yutaro Sato. I also thank those who cooperated with age estimation of chimpanzee, bonobo and Japanese macaque stimuli used in Chapter 2. I also thank Drs. Michio Nakamura, Satoshi Hirata, Toshifumi Udono, Heungjin Ryu, Yumi Yamanashi, Mr. Koshiro Watanuki, Mr. Hiroki Okamura, Mr. Takumasa Yokoyama, and the Wolfgang Köhler Primate Research Center Hirakawa Zoological Park, Higashiyama Zoo and Toyohashi Zoo & Botanical Park, who generously offered me their photos and the information to use as stimuli. I thank members of the Center for International Collaboration and Advanced Studies

in Primatology (CICASP): Drs. Andrew MacIntosh, Yuko Hattori and Susumu Tomiya for their comments for my research output.

The studies were supported by MEXT (17J04125, 15H05709, 18H04194, 16H06283, 16K21108 and 18H05072), JSPS-LGP-U04. The information on the individual participants provided by the Great Ape Information Network (GAIN).

I also thank my family, mother, father, sister for their support and understanding. I'd like to thank Heungjin Ryu for his support and so many scientific discussions we made. I also appreciate all great friends in PRI and other places who discussed or had a good relaxing time with me.

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Abstract

Giving adequate care to infants is critical for their survival in all mammals. Infant visual cues affect parents' decisions for their investment. Specifically, humans recognize infant faces a unique way; for example, infant faces are easily distinguished from adult faces, attract visual attention, and are preferred. Previous studies suggest that these recognitions are related to humans' high sensitivity to infant face shape features called "baby schema," which is presumed to be shared across taxa. To understand the evolutionary pathway of human cognition, it is important to compare humans and non-human primates from a comparative cognitive perspective. Infants of many primate species have a conspicuous coat or skin color different from adults called "infantile coloration." However, psychological effects (e.g., attract attention) of either baby schema or infantile coloration in non-human primates remains unclear. Thus, this thesis explored how great apes recognize infant faces by comparative cognitive approaches and investigated how these species-common (baby schema) and species-specific (infantile coloration) infantile face features affect their responses. I targeted chimpanzees and bonobos, which are phylogenetically closest to humans but have different infant appearances amongst them. This thesis aims to know the evolutionary pathway of humans' recognition of infant faces and test universality and uniqueness of a primary infant face cue in primates.

The first half of the studies investigated great apes' spontaneous visual attention toward infant faces in naturalistic images. Chimpanzees and bonobos were tested with eye-tracking tasks. Chapter 2 examined whether chimpanzees and bonobos have a visual preference for infants of conspecifics and heterospecifics. Eye movements were measured while they looked at images of a mother-infant pair. As a result, chimpanzees viewed the faces of infant conspecifics for longer than they viewed adults but did not show any preference when the facial coloration was matched between infants and adults. Bonobos did not show visual preference for infants. Neither species showed visual preference for infants of heterospecifics. The results indicate a general lack of preference for the species-common infantile features in both species and the importance of the infantile coloration in chimpanzees' visual preference. To understand motivational mechanisms of their visual attention to infants, Chapter 3 investigated how administration of oxytocin affects looking behavior. Chimpanzees and bonobos were administered either oxytocin or saline, and then an eye-tracking experiment was conducted. As a result, the significant effect of the administration condition was not observed in either species. The experimental design and individual differences may account for the absence of the effect of oxytocin administration.

The second half of the studies focused on chimpanzees' face recognition regarding the age category and tested which facial feature, facial shape, or facial color is more important for the recognition. Chapter 4 aimed to reveal the relative contributions of facial shape and color to age categorization in chimpanzees. Chimpanzees were trained to discriminate between adult and infant faces using a symbolic matching-to-sample task. Then, how the categorizations transferred to a series of morphed faces were tested. Image analysis revealed significant differences, both in shape and color,

between adult and infant faces. However, behavioral data showed that facial coloration contributed to age categorization more than facial shape in chimpanzees. Although chimpanzees can discriminate between adult and infant faces, whether they represent conceptual age categories from faces like humans remains unclear. Therefore, Chapter 5 investigated conceptual age categories through spatial mapping of adult and infant faces. Chimpanzees were tested using an identical matching-to-sample task, and whether the response time was influenced by the position and age category of target stimuli was analyzed. The evidence of the spatial representation of the age category was not found. However, the results show that the response time was consistently faster when the chimpanzees discriminated between adult faces than when they discriminated between infant faces. This result is in line with a series of human face studies, suggesting the existence of an “own-age bias” among chimpanzees. To reveal the reason of this asymmetric face discrimination performance, Chapter 6 tested the impairment effect of infant face coloration. I conducted an identical matching-to-sample task and compared the performance among four conditions with facial color and shape were either adult or infant respectively. I found that the facial color, but not the shape, of infants makes the face recognition difficult in chimpanzees. This result again confirms the saliency of infantile face coloration in chimpanzees and further suggests that chimpanzees’ usual and fluent face processing is not advanced due to such salient face features.

The main finding of this thesis is that each species has species-specific visual characteristics of infants and the way of responding to them. Previous studies suggest that human infants advertise themselves by baby schema, facial shape features. On the other hand, chimpanzee infants attract adults by unique face coloration. Meanwhile, bonobo infants do not appear to have particular facial characteristics that attract adults. Although some basic face processing, such as visual preference for infants and face discriminability between and within age categories, are shared between chimpanzees and humans, the primary cues of infant faces are different from humans. These results call for reconsideration of the idea that baby schema has a general effect across species and highlight the need to consider species differences in infant appearance and the sensitivity to it. The infant appearance and adults’ sensitivity to it in each species may be at least partially determined by ethological factors of the species, such as the existence of infanticide or the extent of alloparenting.

Chapter 1: General Introduction

1.1 Infant faces for humans

“As in all innate schemata of man, and probably also in animals, to which one cannot naturally say anything certain about them, the response to the baby schema is also connected with quite certain, autonomous, and incomparable feelings and affects, with a quite specific experience, the quality of which, is usually expressed in German as ‘cute,’ ‘sweet,’ most clearly in southern German as ‘hearty’.”

— Lorenz, 1943 (translated by the author)

1.1.1 Recognition of infant faces in humans

Giving care to infants is important for their survival in all mammals. However, parent and offspring inevitably compete over issues involving differences in optimal parental investment, which is called “parent-offspring conflict” (Trivers, 1974). It is optimal for offspring to demand maximum investment, whereas it is optimal for parents to divide their investment equitably among their offspring. Infants are considered to “employ psychological rather than physical tactics to induce more investment” from their parents (Trivers, 1974, p.257). Meanwhile, parents need to make important decisions on the amount and time of their investment to maximize their fitness. Information about the offspring is highly relevant to these decisions, and it is thought that physical cues of infants, especially facial cues, impact parents’ decisions on the investment (e.g., DeBruine et al., 2016; Volk & Quinsey, 2002). Indeed, human studies have shown for decades that infant faces are perceived in a unique way and seemingly influence “adult’s perceptions and decisions related to parental investment” (e.g., Franklin & Volk, 2017, p. 296).

Humans can easily distinguish between infant and adult faces at a glance. During the development from infant to child, face proportion changes because each facial part grows at different accelerations and the face change continues, to some extent, even after cessation of growth (Kwon & Lobo, 1999). It is suggested that underlying mechanisms of processing adult and infant faces are

independent in humans (Little et al., 2008). Computations for visual age classification revealed that faces can be reliably categorized into infants, young adults, and senior adults by the combination of the two facial features, facial part ratios and wrinkles, and the former is especially important for discriminating between infants and adults (Kwon & Lobo, 1999). Even infants can form age categories from faces (Damon et al., 2016). Damon et al. (2016) tested infants with a visual paired comparison paradigm using images of differently aged faces. The looking time analysis found that both younger (9-month-old) and older infants (12-month-old) formed infant versus adult categories, and older infants formed infant versus child categories as well with a small number of the exemplars. Humans are sensitive to even impoverished age-related facial cues, such as the profile outline of a face (Pittenger & Shaw, 1975). Face discrimination within as well as among an age category has been studied, and the interaction effect between age class of face stimuli and that of participants exist. Such bias for certain age categories is called “own-age bias” (M. G. Rhodes & Anastasi, 2012). That is, discrimination among infant or child faces is more difficult for adults than that among adult faces (e.g., Chance et al., 1986).

Infant faces catch our eyes. For example, infant face stimuli enhance spatial attention in a dot-probe task (Brosch et al., 2007). They briefly presented an adult face and an infant face on the left and right of the monitor, and then the target dot was presented on either of the sides. The participants responded faster to the target dot when an infant face, rather than an adult face, was presented on the same side of the target. Brosch et al., (2008) recorded event-related potentials from the participants performing the same task. The results suggest that infant faces induce attentional orientation relatively early during stimulus processing, which is similar to what emotionally negative stimuli (e.g., an angry face) do. Later studies have almost consistently suggested the existence of attentional prioritization on infant faces, although the type of stimuli, tasks, or participants vary among them (for review Lucion et al., 2017). Importantly, positive correlations between attentional bias toward distressed infant faces and the quality of mother-infant relationship is reported (Lucion et al., 2017). Therefore, attentional priority

to infant faces may increase infant fitness by facilitating parenting behavior. Additionally, infant faces hold as well as capture our attention. Attention holding effect of infant faces is reported by eye-tracking experiments. In Cárdenas et al. (2013), an adult face and an infant face were presented to participants, whose eye movements were recorded. As a result, participants, especially females, looked at infant faces longer than adult faces. It should be noted that the word “visual preference” is also used, but it refers to a state where one’s attention is attracted by something instead of a state one finds pleasant.

Infant faces induce not only fast and autonomic processing, such as visual attention, but also slow processing, including positive appraisal (Kringelbach et al., 2016). Studies have shown that infant faces are preferred and induce affiliative emotions, especially perceptions of “cuteness” (e.g., Heron-Delaney et al., 2018; Little, 2012; Lorenz, 1943; Senese et al., 2013). For example, a behavioral study reported that infant faces are implicitly associated with positive emotions (Senese et al., 2013). Neurological studies also support that infant faces work as reward. Magnetoencephalography (MEG) shows that specific brain areas involving reward processing are activated when participants look at an infant face but not an adult face (Hahn & Perrett, 2014; Kringelbach et al., 2008). Participant gender difference is reported for rewarding value of looking at infant faces, which are typically preferred more by females than males (e.g., Hahn et al., 2013; Maestriperieri & Pelka, 2002). Moreover, hormonal regulation of women’s responses to infant facial cuteness has been reported (for review DeBruine et al., 2016). Although infants are generally perceived as cute, the influence of the difference of cuteness among infants on cognitive and behavioral response is noteworthy. Golle et al. (2015) presented cuter and less cute infant faces to participants and asked them to choose the infant to whom they would rather give a toy and adopt. They found that cuter infants were chosen more frequently. They also examined the perceived cuteness and perceived health, and found a significant relationship between health and cuteness evaluation of infant stimuli, as reported also by other studies (e.g., Volk & Quinsey, 2002). Therefore it is presumed that cute infants may be preferred because the cost of raising cute and seemingly

healthy infants should be smaller. Positive appraisal as well as visual attention toward infants are supposed to be major cognitive mechanisms underlying infant care in humans.

1.1.2 Shape features of infants—Baby schema

Infant faces are easily discriminated from adult faces, attract attention, and are preferred by humans. Then, what makes infant faces special? “Baby schema¹ (*Kindchenschema*, Lorenz, 1943)” is one of the most famous characteristics of infant appearance. Prominent ethologist, Konrad Lorenz, suggests that infant faces have a set of physical features observed across species and induce caretaking behavior (Lorenz, 1943). Lorenz defined infantile features, such as relatively bigger eyes and forehead, protruding cheek, and small nose and mouth as baby schema. Since the existence of baby schema was established, several studies have demonstrated human’s high sensitivity to baby schema. The extent of baby schema affects attractiveness of the face as well as perceived age (Pittenger & Shaw, 1975). Studies have suggested that exaggeration of baby schema makes the face more appealing and increases caretaking motivation when participants were asked to rate face images (Alley, 1981, 1983b; Glocker, Langleben, Ruparel, Loughhead, Gur, et al., 2009; Hildebrandt & Fitzgerald, 1979; Sternglanz et al., 1977). A study using functional magnetic resonance imaging (fMRI) found that seeing infant faces with high-baby schema activates the nucleus accumbens, which is mediating reward processing (Glocker, Langleben, Ruparel, Loughhead, Valdez, et al., 2009).

Humans also found infant faces of other species are attractive (e.g., Maestriperi & Pelka, 2002). This is thought to be because baby schema is morphologically shared among not only humans but also various mammalian and avian species (Lorenz, 1943). Indeed, baby schema also influences non-human animal faces as well as human faces for human perception (Borgi et al., 2014; Borgi & Cirulli, 2013; Golle et al., 2015; Little, 2012; Pittenger & Shaw, 1975). For example, dog and cat faces are perceived as cuter by humans when baby schema of the faces is exaggerated (Borgi et al., 2014; Little, 2012). In Golle et al., (2015), people were asked to rate the cuteness of human infant faces, after

adaptation of cute or less cute infant faces of either humans or dogs. As a result, adaptation to cute and less cute puppy faces as well as human faces affected the subsequent cuteness rating in human infant faces. Golle et al., (2015) argued that this result indicates the existence of a mechanism underlying human processing of infant cuteness across species. Furthermore, human preference for baby schema is even observed for artificial objects such as cartoon characters (Gould, 1980) and cars (Miesler et al., 2011). These studies suggest that humans prefer baby schema and such preference is not limited to conspecifics but is generalized to hetero species or artificial objects. The preference for baby schema, which is seemingly shared by a wide range of species, is thought to explain why humans have a general preference for infants.

In humans, not only adults but also children, who are too immature to take care of infants, already show preference for baby schema (Borgi et al., 2014; Sanefuji et al., 2007). In Borgi et al., (2014), baby schema in face images of humans, dogs, and cats were manipulated and presented to children aged 3 to 6 years. As a result, baby schema affected children's cuteness rating and gaze allocations. The existence of such preference for infantile face features in children is congruent with the idea that baby schema is an innate releasing mechanism for caretaking behavior (Lorenz, 1943). However, we should be cautious about concluding that preference for baby schema is innate, since children may be influenced by the culture surrounding them and experiences including cartoon characters with exaggerated baby schema. Moreover, if baby schema is equipped in infants across taxa as an innate releaser of caretaking in general, baby schema recognition should be shared with non-human animals as well as humans. Surprisingly, however, it has not been tested whether baby schema works (e.g., affects age recognition, is preferred, or induces caretaking motivation) in non-human animals.

1.2 Infant visual stimuli for non-human primates

1.2.1 Response to infant images in non-human primates

In order to understand the evolutionary pathway of humans' recognition, it is important to compare humans and non-human animals. Getting information from infants should be also important for other mammalian species because it will affect the parents investment. Among animals, it is reasonable to expect that non-human primates are responsive to infantile visual features, including baby schema, because they generally rely on visual cues compared with other modalities like humans. Although it is unclear which visual feature of infants is particularly important, studies are testing non-human primates' responses to infant visual stimuli.

First, visual preference for infants has been demonstrated with a few primate species. Early work by Sackett (1966) tested rhesus macaques reared in isolation and measured their responses (i.e., exploration, play, vocalization, and disturbance) to various images including those of infants. The monkeys responded more to threat and infant images compared with other images (e.g., fearful or sexual conspecific images). Thus, it was concluded that visual stimuli of infants are socially meaningful for rhesus macaques by nature. Visual preference for conspecific infants in non-human primates was demonstrated in other species too. Sato et al. (2012) presented whole body pictures of adult and infant Japanese macaques to participants of Japanese macaques and Campbell monkeys using a visual paired comparison task. As a result, Japanese macaques looked more often at novel images as a first look and the total looking time was longer for infant images compared with adult images. Campbell monkeys also looked at infant Japanese macaque images for longer duration although there is no difference in the first look. The results indicate that both species can discriminate infants and adults of Japanese macaques and have visual preferences for infants. Visual preference for infants was also reported in barbary macaques (Almeling et al., 2016). Although interpreting the meaning of such visual preference for infants is typically difficult by itself, rewarding value of infant visual stimuli was reported in common

marmosets. Pryce et al. (1993) examined maternal motivation of female marmosets by operant conditioning paradigm and investigated the effect of the hormonal states on it. In this paradigm, pressing a lever resulted in (a) getting visual access to an infant replica and/or (b) turning off the playback of infant distress calls. Marmosets learned the operant behavior, and the frequency of the behavior was increased by the treatment of progesterone and estradiol mimicking late-pregnancy steroid profiles. This study offers several implications, including that visual stimuli of infants work as rewarding stimuli and that maternal motivation is influenced by sex steroids in marmosets.

Although those previous studies used whole body images as infant stimuli, faces may particularly convey important cues of infants in non-human primates too. This is because it has been shown that non-human primates can extract various information from faces (Adachi & Tomonaga, 2017; Leopold & Rhodes, 2010; Parr, 2011). However, fewer studies tested primates' responses, particularly toward infant faces. Koda et al., (2013) tested whether Japanese macaques show the rapid spatial orientation toward infant faces that is reported in humans (Brosch et al., 2008) by using a dot-probe task. However, they did not find such evidence. Considering that visual preference for infants is observed in non-human primates, infant faces may hold but not capture their attention. Otherwise, presenting face without whole body may not be enough to affect visual attention. On the other hand, Kawaguchi, Kuroshima, et al., (2019) demonstrated that capuchin monkeys can discriminate between adult and infant faces of conspecifics and humans. They trained capuchin monkeys to match adult or infant faces and the corresponding geometric figure by a symbolic matching to sample task. The monkeys successfully learned the categorization, but it did not transfer to other species faces without additional training. Therefore, capuchin monkeys extracted shared visual features within each age category during the training, but the cues they used were species-specific. These two studies are the only ones to investigate non-human primate visual processing of infant faces.

1.2.2 Color features of infants—Infantile coloration

Importantly, many (but not all) primate species have a conspicuous coat or skin color that is different from adults known as infantile coloration (Alley, 1980; Hrdy, 1976; Ross & Regan, 2000; Treves, 1997). The coloration and its conspicuousness vary among species. According to Treves (1997), approximately half of primate species have such infantile coloration. The adaptive function of infantile coloration attracts researcher interest because conspicuous coloration seems maladaptive, since it may stand out to predators and advertise an infant's vulnerability. Some researchers regard infantile coloration as a "tactic" by which infants induce care from adults around them (Alley, 1980; Hrdy, 1976; Ross & Regan, 2000). However, other researchers do not agree and consider the function of infantile coloration as preventing aggression toward infants or hiding phenotypic cues indicating paternity (Trivers, 1974). Thus, there is no consensus on functional mechanisms of infantile colorations.

Although observational studies suggested that animals seemingly change behavior toward infants with and without infantile coloration (e.g., Poirier, 1968; van Lawick-Goodall, 1968), those studies typically failed to control for other factors such as actual age of infants. Experimental study can potentially solve this issue, but there are only two empirical attempts to investigate primate response to infantile coloration. Gerald et al. (2006) and Higley et al. (1987) experimentally investigated rhesus macaques' responses to infantile coloration, but the two studies did not result in a consensus. Higley et al., (1987) presented female macaques with conspecific infants whose face and/or fur was dyed and investigated approach behavior. They found that neonatal-like facial skin coloration especially attracted females. Gerald et al., (2006) also tested the role of neonatal color by presenting digitally color-manipulated face images to female macaques. However, they found that neonatal facial color did not particularly attract females. Thus, it remains unclear how primates respond to infantile coloration.

1.3 Aim of the thesis

The aim of the thesis is to reconstruct the evolutionary pathway of humans' recognition of infant faces and test universality and uniqueness of a primary infant face cue in primates. Experimental examination of nonhuman primates' responses to infant faces has been insufficient (Kawaguchi et al., in press). Specifically, it remains unclear which particular feature is an important cue of infants, because previous experimental studies presented whole body images of infants without control as stimuli (Almeling et al., 2016; Pryce et al., 1993; Sackett, 1966; Sato et al., 2012). On the one hand, baby schema, a set of infantile face shape, is believed to affect non-human primates (and other mammals) as well as humans without empirical tests. On the other hand, the other infant feature, infantile coloration is also believed to be a critical visual cue of an infant. Thus, it is unclear whether these visual features of infants play a significant role or they are irrelevant when non-human primates recognize infants. Facial shape and color are the most important properties in face processing in general for both humans and chimpanzees (Parr et al., 2012; G. Rhodes et al., 2011). Therefore, in this thesis, I segregated and compared the effect of facial shape (baby schema) and facial color (infantile coloration).

This thesis targeted the two species of great apes, chimpanzees and bonobos, for three reasons. First, they are phylogenetically closest to humans. Thus, testing great apes will elucidate how much humans' way of recognizing infant faces are preserved or uniquely acquired during evolution. It plays an essential role to reconstruct the evolutionary scenario on how the way humans recognize infants evolved. Second, chimpanzees, but not bonobos, have infantile coloration, which humans do not have (Napier & Napier, 1967). Figure 1.1 illustrates average adult and infant faces of chimpanzees and bonobos. There is a conspicuous color difference between adult and infant faces in chimpanzees but much less conspicuous color difference in bonobos. Testing both species with and without infantile colorations is necessary to test whether primates use species-specific or species-common characteristics as the primary infant face cue. Third, chimpanzees and bonobos are different from humans and from

each other in behaviors toward infants. The frequency of infanticide varies. No infanticide has been reported in bonobos (T. Kano, 1998), while it has been reported in chimpanzees (M. L. Wilson et al., 2014) and humans (Hausfater, 1984). The extent of infant care by non-mothers also varies. Humans are unique in terms of the broad and extensive cooperative breeding system (e.g., Burkart & van Schaik, 2010; Kramer, 2005). Meanwhile, alloparenting exists in both species (Bădescu et al., 2016; Boose et al., 2018); however, the extent of it is quite low even compared with other non-human primates (Burkart & van Schaik, 2010). These ethological factors can be relevant to the responsiveness toward infant stimuli in each species. In summary, the phylogenetical similarities and the morphological and ethological differences among species make chimpanzees and bonobos good species to test and compare with humans.

In this thesis, I tested chimpanzees in Chapters 2–6 and bonobos in Chapters 2 and 3. Chapters 2 and 3 adopted eye-tracking tasks, which are useful tools to investigate animal's spontaneous visual preference without training. Chapters 4, 5, and 6 adopted touch-panel tasks, more specifically matching-to-sample tasks. Touch-panel tasks are useful to test various animal cognitive aspects explicitly, including subtle sensitivity to differences and similarities among stimuli. In Chapter 7, the results of the five studies are summarized, and the similarities and differences between humans and great apes are discussed. In this thesis, I tried to understand great apes' recognition of infant faces from the following three aspects (Figure 1.2).

Visual attention to infant faces in naturalistic images (Chapters 2 and 3)

Faces do not exist alone in nature. Do infant faces attract great apes' attention in naturalistic images? I investigated chimpanzees' and bonobos' spontaneous visual preference for infant faces versus adult faces by measuring eye gaze. In Chapter 2, by using both conspecific and heterospecific stimuli and color-controlled stimuli, I compared the role of species-common and species-specific infantile

features in great apes' visual preference. To interpret the meaning of visual preference further, Chapter 3 investigated the effect of hormone on the visual preference. I tested how administration of oxytocin, which is known to regulate parenting behavior, affects great ape's visual attention to adults and infants.

Primary cues in face discrimination between and within age categories (Chapters 4 and 6)

Then I asked main questions, which serves as a more important cue of an infant face, baby schema or infantile coloration? Chapters 4 and 6 focused on chimpanzees' face discrimination between and within age categories and tested which facial feature, facial shape or facial color, is more important for the discrimination. Chapter 4 adopted a symbolic matching task, and chimpanzees were trained to categorize adult faces and infant faces. Then I tested how two facial features, namely shape and color, contribute to the discrimination by using morphed images.

Although investigating face discrimination between age categories was achieved in Chapter 4, asymmetric efficiency on face discrimination within age category was found between adults and infants in Chapter 5. That is, discriminating among adult faces was easier than discriminating among infant faces. Therefore, Chapter 6 further tested the role of facial color versus shape on the face discriminability and examined the reason of the difficulty of discriminating infant faces for adult chimpanzees.

Conceptual age category from faces (Chapter 5)

I used face stimuli but it is not obvious that chimpanzees recognize faces as "adults" and "infants," as humans do. Although chimpanzees can visually discriminate between adult and infant faces, it remains unclear whether chimpanzees represent conceptual age categories from faces. Therefore, Chapter 5 tested whether chimpanzees have spatial representation of faces of adults and infants.

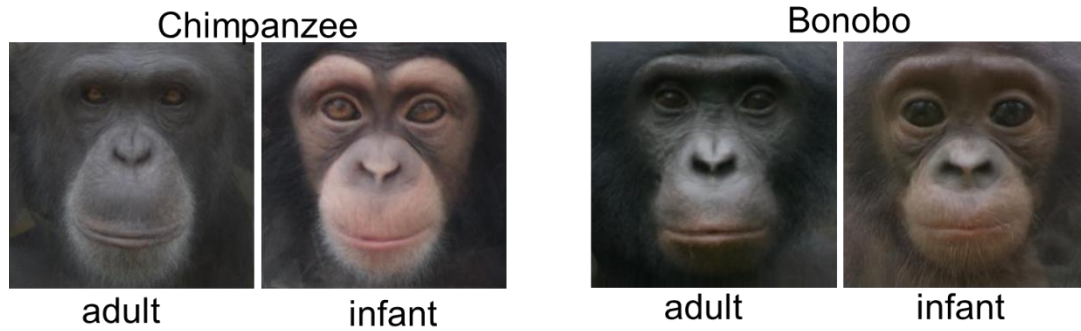


Figure 1.1 Variation of conspicuousness of infantile coloration. A) An average adult face and infant face of chimpanzee (left) and bonobo (right).

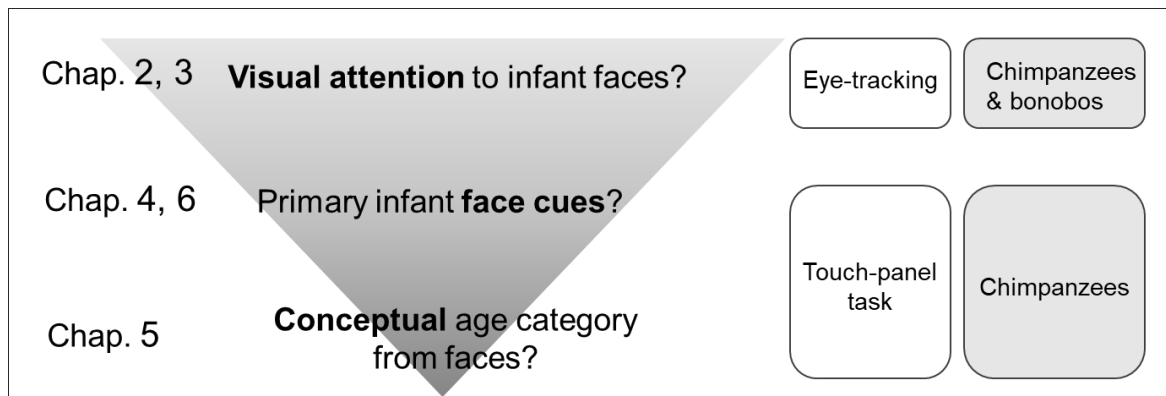


Figure 1.2 The structure of the studies.

Note

*1. In previous literature, the term “baby schema” was used in various ways (e.g., just referring to an “infant face”). However, not all facial features of infants are shared among various species, and an aim of this thesis is to compare infantile features that are species-specific versus species-common.

Therefore, in this thesis I will use this term “baby schema” in a narrow and original sense, namely, a set of morphological features defined by Lorenz (1943) and supposed to be widely shared across species.

Chapter 2: Chimpanzees, but not Bonobos, Attend

More to Infant than Adult Conspecifics

This chapter was published in the journal: Kawaguchi, Kano & Tomonaga (2019) *Animal Behaviour*, 154, 171–181. doi: 10.1016/j.anbehav.2019.06.014

2.1 Introduction

In many animal taxa (e.g., birds and mammals), infants can be reliably distinguished from adults by their appearance. For example, they are smaller than adults and clumsier in movement. A well-known example is ‘*Kindchenschema* (baby schema)’, which is a set of morphological features commonly observed across species, such as relatively large eyes, a large head, a high and protruding forehead, rounded cheeks, and a small nose and mouth (Lorenz, 1943). In addition to this baby schema, some species of nonhuman primates have conspicuous skin and coat coloration (Alley, 1980; Booth, 1990; Hrdy, 1976; Treves, 1997). For example, silvery langur infants, *Trachypithecus cristatus*, have an orange coat and pale skin, in marked contrast to the black-and-white coat and dark skin of the adults. Unlike baby schema characteristics, such conspicuous coloration of primate infants is unique to each species. Therefore, infants of these primate species have both species-common (e.g., body size, baby schema) and species-specific features (e.g., conspicuous coloration). The apparent functions of baby schema and conspicuous infantile coloration are to capture attention and increase motivation for caretaking (Alley, 1983b, 1983a; Glocker, Langleben, Ruparel, Loughhead, Gur, et al., 2009; Hrdy, 1976; Sternglanz et al., 1977). Although there is a large body of literature showing that humans are attracted to the baby schema of both conspecifics and heterospecifics, it remains unclear whether nonhuman primates are also attracted to the same species-common features. Moreover, it remains unclear which infantile features, particularly species-common (e.g., a relatively large head and eyes) or species-specific features (e.g., conspicuous coloration), are more attractive to species with and without special infantile

features. In this paper I aim to clarify this problem by presenting first an overview of the literature and then the results of an experiment testing the effect of infantile features in bonobos, *Pan paniscus*, and chimpanzees, *Pan troglodytes*; these two closely related ape species differ in several key aspects, which might help answer the questions raised.

In humans, several experimental studies have examined the effects of infantile features on cuteness perception, motivation, physiology and reward processing in the brain. Although some of these studies focused on auditory or olfactory cues (Kringelbach et al., 2016), most focused on visual features, especially the baby schema. For example, humans typically rate human infants with a stronger baby schema as more attractive, and they express a stronger motivation to take care of them (Alley, 1983b; Glocker, Langleben, Ruparel, Loughhead, Gur, et al., 2009; Sternglanz et al., 1977). Importantly, humans rate heterospecific infants with strong baby schema similarly (Borgi et al., 2014; Little, 2012). Studies using nonverbal methods, such as eye tracking and key press tasks, have shown that humans display stronger motivation to view images of human infants over those of adults (Cárdenas et al., 2013; Hahn et al., 2013) or heterospecific faces (dog and cats) with a strong baby schema (Borgi et al., 2014). Physiologically, human adults are aroused when they see the faces of infants, as indicated by temperature increases in their facial skin (Esposito et al., 2014, 2015). Functional magnetic resonance imaging shows that neural structures mediating reward processing and appetitive motivation are activated when women see strong baby schema faces (Glocker, Langleben, Ruparel, Loughhead, Valdez, et al., 2009; for a review, see Kringelbach et al., 2016; Young et al., 2017). Many of these studies have reported gender differences, in that females generally show stronger responses to infants than males (Cárdenas et al., 2013; Esposito et al., 2015; Hahn et al., 2013; Proverbio et al., 2011).

In nonhuman primates, although more limited in number, several experimental studies have examined the attraction of adults to infants. For example, Almeling et al., (2016) showed that adult male and female Barbary macaques, *Macaca sylvanus*, looked longest at images of newborns when presented

with images of newborns, close friends or nonfriend adults. However, the motivation of this species to view these images might differ from that of humans because, in this species, infants are occasionally used as a social tool to facilitate interactions among males (Henkel et al., 2010). Sato et al., (2012) found that adult female Japanese macaques, *Macaca fuscata*, were more attracted to conspecific images of infants than those of adults. When adult female Campbell's monkeys, *Cercopithecus campbelli*, were tested with the same images of Japanese macaques, they were also more attracted to the macaque infants. Thus, the authors suggested that, at least, Campbell's monkeys are attracted to the species-common baby schema. However, as the authors did not adopt a full cross-species design in which the two species viewed both conspecific and heterospecific infants, it remains unclear whether they were attracted to the species-common or the species-specific features (e.g., pale skin and dark coat) of the macaque infants.

Primatologists have studied the function of conspicuous infantile coloration in some species of primates. Early reviews pointed out that such infantile coloration has certain effects on the behaviors of both kin and nonkin adults; specifically, this trait might facilitate alloparental attention and care, and prevent aggression from infanticidal adult males (Alley, 1980; Hrdy, 1976). This hypothesis is primarily based on several observational reports. For example, male chimpanzees might inhibit their aggression when they see an infant with a white tail tuft on the mother's back (van Lawick-Goodall, 1968). In addition, adult chimpanzees become less tolerant to juveniles (older than about 4 years) when they start to lose infantile features, such as the white skin color and tail tuft (van Lawick-Goodall, 1968). Female Nilgiri langurs, *Trachypithecus johnii*, often carry another's infant, and this behavior was found to decline as infants' skin and coat color became more like those of adults (Poirier, 1968). Female ursine colobus, *Colobus vellerosus*, more frequently handle conspecific young infants with white or grey coats than they do older infants with black-and-white coats (Bădescu, Sicotte, Ting, & Wikberg, 2015).

Species-wide surveys, however, have failed to identify a clear function of conspicuous infantile coloration. These studies tested the correlation between infantile features and the level of

alloparental care, predation risk, and mating and social systems. In a study of 138 species, Treves, (1997) found no correlation between infantile coloration and alloparental care, but a significant correlation between infantile coloration and mating system, which is presumably related to the level of male aggression. However, when controlling for phylogenetic bias, Ross & Regan (2000) found no significant correlations, and only a weak, nonsignificant correlation with alloparental care. One possible explanation for the lack of correlation in these studies is that the effects of infantile coloration may be too subtle to be analyzed in the surveys, if it causes, for example, increased attention, general tolerance and an inhibition of aggression. Experimental studies controlling infantile colors might help to resolve the issue.

There are two such experimental studies with rhesus monkeys, *Macaca mulatta*. One study examined the approach responses of adult females to infants whose faces and/or coats were dyed to mimic neonatal coloration (Higley et al., 1987). Adult females stayed for longer near dyed than nondyed infants, especially those with dyed faces. This effect was not due to novelty because the females did not spend much time with infants dyed an unnatural color. Another study examined the preferential looking at and approach of adult rhesus females to facial images of both neonates and infants (Gerald et al., 2006). The images were manipulated to mimic the color of neonates, unaltered or unnatural. Unlike Higley et al., (1987), this study found no preference of females for images with neonatal facial color; however, females stayed for longer with images of infants (of any color) compared to neonates. The authors suggested that infantile coloration is not particularly important in mediating infant attractiveness to female rhesus adults as previously suggested, or that other age-related infantile facial features might be more important.

In this study I aimed to further clarify whether previously untested bonobos and chimpanzees have any preference for infants and, if so, whether they are attracted to species-common features (e.g., a relatively large head and eyes) or species-specific features (e.g., conspicuous coloration). I followed

the approach of Almeling et al., 2016, Gerald et al., 2006, and Sato et al., 2012, in that I examined viewing preferences but with modifications to their protocols. Specifically, I used eye tracking, so that participant primates could examine naturalistic scenes rather than trimmed faces/bodies. In addition, I used a full cross-species design, in which the two species viewed the images of both species and an outgroup species (Japanese macaques) to distinguish between their attraction to species-common and species-specific features. I tested bonobos and chimpanzees for several reasons. First, as far as I know, these species have never been experimentally tested for their preference for infants. Second, they are phylogenetically closer to humans than monkeys and, therefore, the data will add valuable knowledge to a broader comparative picture. Third, they are closely related; however, despite their general similarities, they differ morphologically, behaviorally and socioecologically in significant ways (Furuichi, 2011; Hare et al., 2012). Of particular interest is that they differ in the presence/absence of infantile coloration and severe aggression towards infants.

Both species are similar in that the infants experience a long period of dependence on their mothers and other group members, which are generally tolerant of in-group infants, travelling and feeding together and playing with them (de Lathouwers & van Elsacker, 2006; van Lawick-Goodall, 1968). Cases of adult males adopting orphans have even been reported in chimpanzees (Boesch et al., 2010; Thierry & Anderson, 1986). However, severe aggression towards infants, including infanticide, is also common in chimpanzees (M. L. Wilson et al., 2014), but rare in bonobos (T. Kano, 1998). Chimpanzee mothers often leave their group after giving birth, so-called ‘maternity leave’ (Nishida et al., 1990), which may be a counterstrategy against infanticide (Nishie & Nakamura, 2018). Bonobo mothers, by contrast, interact more freely with various group members (Doran et al., 2002), and they also break body contact with their infants more frequently than chimpanzee mothers (de Lathouwers & van Elsacker, 2004). Morphologically, chimpanzee infants have special conspicuous coloration, namely pale skin and white tail tufts, which adults do not have. Bonobo infants are not distinguished from adults

in coloration, both having dark skin. Both infant and adult bonobos have white tail tufts like chimpanzee infants. Interestingly, bonobo adults tend to retain juvenile features in general, such as short snouts, possibly as an effect of domestication-like processes in bonobo evolution (Lieberman et al., 2007). One interesting hypothesis, therefore, is that the special infantile coloration of chimpanzees may have evolved as a strategy to reduce the risk of aggression, including infanticide, and to attract attention from conspecific adults. Such signals may be less important in bonobos, since this species does not have infanticide, and therefore these signals did not evolve or lost their original function during evolution.

I predicted several possible results. First, if species-common infantile features (e.g., a large head and eyes) are the most influential, both species would be attracted to the infants of all species, including Japanese macaques. Second, if both species are generally attracted to conspecific infants for some reason; for example, due to the specialized processing systems of primates for conspecific faces (Dufour et al., 2006; Dufour et al., 2004; Pascalis, 2002), they would look longest at conspecific infants. Third, if special infantile coloration generally catches attention simply by standing out, both species would look at chimpanzee and macaque infants for longer than at bonobo infants. Finally, if the infantile coloration of chimpanzees has a special meaning to conspecifics, chimpanzees but not bonobos would show a preference for looking at chimpanzee infants, but only when they exhibit special infantile coloration.

2.2 Methods

2.2.1 Participants

Fifteen chimpanzees, *P. t. verus* (aged 9–51 years) and six bonobos (aged 13–46 years), all adults or adolescents, participated in experiments 1–3 (see Table A2.1 for more details). The same chimpanzees (but not bonobos) participated in experiment 4. Four chimpanzees and two bonobos were males. Six chimpanzees and all bonobos lived at the Kumamoto Sanctuary (KS); nine other chimpanzees

lived at the Primate Research Institute (PRI), Japan. KS chimpanzees and bonobos lived separately, but with occasional mutual visual access. Neither species in KS had visual access to macaques. PRI chimpanzees lived separately from, but had daily visual access to, rhesus macaques, including infants; they had no visual access to bonobos. All participants had experience of interacting with conspecific infants. Five female chimpanzees and all four female bonobos had experience of giving birth. All participants had some experience of watching naturalistic images and movies for enrichment and experiments but had never been trained for gaze behavior.

Ethical note

All experiments were conducted in experimental booths (PRI: 1.8 × 2.15 m and 1.75 m high; KS (chimpanzee): 3 × 3 m and 2 m high; KS (bonobo): 3 × 6 m and 3 m high). Chimpanzees were housed in an enriched environment with an outdoor compound (PRI: 700 m²; KS: 1200 m²) equipped with climbing structures and vegetation attached to an indoor enclosure. PRI chimpanzees also had access to a semi-outdoor residence (Matsuzawa, 2006). Bonobos in KS were housed in an enriched semi-outdoor residence (200 m²), which they could freely use in a three-dimensional way. Participants were neither food nor water deprived and they lived in social groups consisting of 6–11 individuals. They received food (fresh fruits, vegetables, sweet potatoes and nutritionally balanced biscuits) several times each day and had access to water any time. The participants were called upon for daily experiments, and their participation was voluntary. All procedures adhered to institutional guidelines (PRI: Primate Research Institute 2002 version of ‘The Guidelines for the Care and Use of Laboratory Primates’; KS: Wildlife Research Center ‘Guide for the Animal Research Ethics’). The experimental design was approved by the Ethics Committee of the Wildlife Research Center (WRC-2017-KS002A), Animal Welfare and Animal Care Committee of the PRI (2017-176, 2018-115) and the Animal Research Committee of Kyoto University.

2.2.2 Apparatus

Eye gaze was recorded using an infrared head-free Tobii eye tracker (60 Hz; X300; Tobii Technology AB, Stockholm, Sweden). Stimulus images were presented at a resolution of 1280×720 pixels on a 23 inch LCD monitor (ca. 43×24 degree) using Tobii Studio software (version 3.2.1) at a viewing distance of approximately 70 cm. The eye-tracker and the monitor were set up outside the experimental booth, and the eye movements of participants were recorded through a transparent acrylic panel (1–2 cm thick). To minimize head movements during stimulus presentation, participants could sip drops of grape juice through a nozzle and tube attached to the acrylic panel. Automated calibration was conducted for each participant by presenting two small images or video clips on each reference point before the test session. I evaluated the calibration accuracy by visually inspecting the differences between the participant's gaze and a few reference points (small images), and I repeated the calibration if necessary. Following these procedures, calibration errors were typically within one degree (Hirata et al., 2010; F. Kano et al., 2011).

2.2.3 Stimuli and Procedure

Experiment 1 (presenting conspecific images)

I presented 20 conspecific images to chimpanzees and bonobos. Each image depicted a mother–infant pair in a naturalistic background (Figure 2.1). The photographs were taken by the authors, provided by colleagues or taken from public sources, and were then edited in Adobe Photoshop Elements 15 to optimize their frames, sizes, brightness and colors. I selected images primarily depicting the faces of both infants and mothers. This was because I was primarily interested in the responses of the apes to faces in the images, as faces have both species-common features (e.g., baby schema) and species-specific features (infantile coloration). I also selected the images depicting infants clearly showing their pale skin colors. Because chimpanzee infants start to lose their infantile features around 4 years old, all

depicted infants were probably younger than this (but could have been slightly older, depending on individual differences in appearance). The infant tail tufts were not depicted (hidden on the backside of their bodies) in most of the images (except for one chimpanzee and one bonobo image). All depicted individuals were unfamiliar to the participants and showed neutral facial expressions. Gaze directions (either straight or slightly oblique to the camera) were matched for the mother and infant. The size of the depicted faces of infants and mothers varied slightly across images; thus, this variation was balanced as much as possible between the chimpanzee and bonobo images. To estimate the ages of depicted infants, I asked experts on chimpanzees and bonobos to rate their approximate age. The experts had to select one of the following options: (1) 0–1 month old, (2) 1 month old–1 year old, (3) 1–2 years old, (4) 2–3 years old and (5) over 3 years old. Nine and five experts rated the chimpanzee and bonobo images, respectively. The overall estimated median age class was 3 (1–2 years old) for both chimpanzee and bonobo images (see Appendix for more detail).

I presented the entire set of 20 images across 2 consecutive days (10 images per day), separating the entire set into two blocks. The order of presenting images within each block and the order of presenting the two blocks were counterbalanced across individuals. Images were presented as a slideshow (i.e., without any interstimulus interval). Each image was presented for 4 s; thus, one session lasted for 40 s. The whole procedure (e.g., sitting in front of the monitor, initiating drinking juice, calibration) lasted for 3–5 min for each individual. The chimpanzees in PRI participated in other tasks (e.g., computerized touch-panel cognitive tasks) before or after participating in this test, but had never seen the same images, and had not been trained in a way that might skew their viewing patterns to the images of either infants or adults in those tasks.

Experiment 2 (presenting heterospecific ape images)

I presented the same 20 bonobo stimuli to the chimpanzees, and the same 20 chimpanzee

stimuli to the bonobos. The procedure used to present stimuli was the same as that in experiment 1.

Experiment 3 (presenting outgroup monkey images)

I showed 20 images of Japanese macaques to both chimpanzees and bonobos following the same criteria as in experiments 1 and 2. Infants of Japanese macaques have pale skin and a dark coat which distinguish them from adults, similar to chimpanzee infants. I selected images depicting infants clearly showing their pale skin. As Japanese macaque infants start to lose their infantile features at around 3–4 months of age (Hamada & Yamamoto, 2010), the depicted infants tended to be younger than chimpanzee and bonobo infants. The backside of infants was not depicted in most images (except two). I asked five experts on Japanese macaques to rate the approximate age of depicted infants in each image in the same way as in experiments 1 and 2, with the following options: (1) 0–0.5 years old, (2) 0.5–1 years old, (3) 1–2 years old, (4) 2–3 years old and (5) over 3 years old. I adopted as similar criteria as possible to those used in experiments 1 and 2, but changed the age ranges for classes 1 and 2, following the suggestion of experts, as distinguishing between newborns and young infants is often difficult. The overall estimated median age class was 1 (0–0.5 years old; see Appendix for more detail). The procedure followed to present stimuli was the same as that in experiments 1 and 2.

Experiment 4 (presenting brightness-matched images)

To examine the effect of infantile coloration, the 20 chimpanzee mother–infant images were first converted to greyscale, and then the global brightness of adult and infant faces was matched as closely as possible (so that infant faces became darker and adult faces became brighter) using the histogram function of Photoshop. I conducted this experiment at least 1 month after experiment 1 to avoid the chimpanzees becoming habituated to the stimuli. I confirmed that the overall viewing times to the stimuli did not differ between experiments 1 and 4 (i.e., the main effect of experiment was not

significant; see Results).

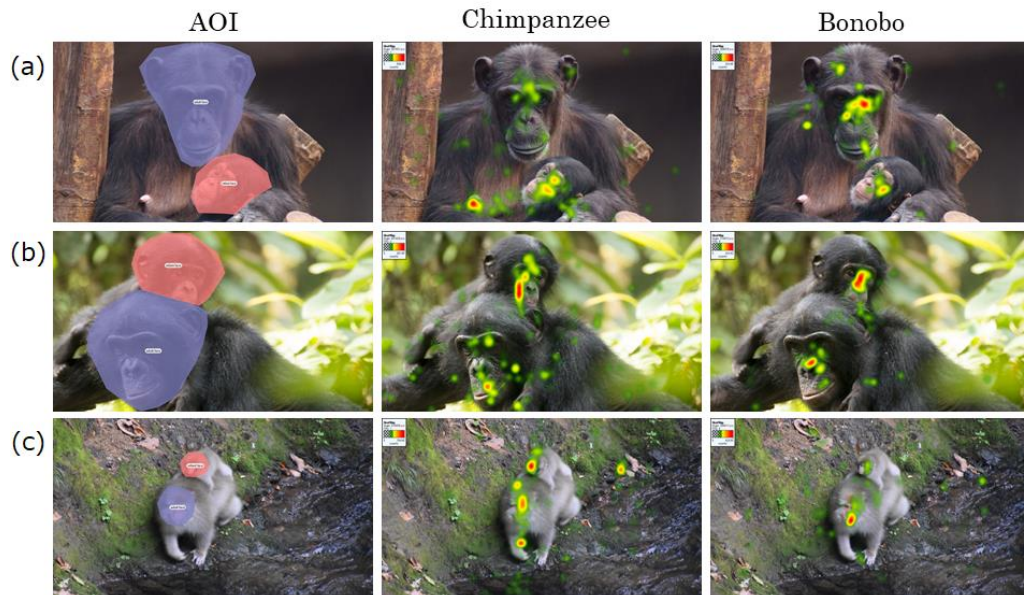


Figure 2.1. Example areas of interest in faces and viewing patterns by chimpanzees and bonobos, represented as a heat map (redder parts indicate more aggregation of fixations); these are superimposed on the images of (a) chimpanzees, (b) bonobos and (c) Japanese macaques.

2.2.4 Data Analysis

Viewing-time analysis

Areas of interest (AOIs) were defined for the faces of infants and adults (Figure 2.1), and the total viewing time for each AOI was analyzed using Tobii Studio (ver. 3.2.1). AOIs were drawn slightly larger than the actual facial sizes (about 20% larger) to accommodate any fixation errors. Eye movement data were filtered using a Tobii fixation filter. Note that adult faces (and the defined AOIs) were generally larger than infant faces, and thus potentially accommodated more fixations. Additionally, the faces of chimpanzee infants were brighter than those of adults, and thus potentially caught more attention. I did not manipulate these factors in experiments 1–3 to keep the infantile signals as natural as possible

(including relative size). Instead, I quantitatively estimated the amount of attention based on those low-level properties using the saliency model, as detailed below.

To examine the viewing bias of participants for adult and infant faces and any species differences, I conducted a repeated-measures ANOVA (analysis of variance) for each experiment (1–3) with participant species (chimpanzee or bonobo) as the between-subject factor and AOI (adult or infant) as the within-subject factor. When I found a significant interaction, I conducted *t* tests to investigate the simple effects of each factor. In experiment 4, I first checked whether the chimpanzees differentially viewed infant and adult faces using a *t* test (two-tailed), and then compared the data with those from experiments 1 (with original images) and 4 (with brightness-matched images) using ANOVA with AOI (adult or infant) and experiment (brightness-matched or original) as within-subject factors, to directly test the effect of color control. All statistical analyses were conducted using R 3.5.1 (R Core Team, 2018).

Saliency analysis

Although the primary strategy to examine the effect of infantile coloration was conducted using a cross-species comparison, a computer simulation of eye movement based purely on low-level image conspicuousness would further help to distinguish between the effect of low-level image conspicuousness and that of infantile coloration on eye movement. Thus, I used a well-established saliency model (Itti & Koch, 2000), which predicts the location of fixations based on low-level visual features, specifically color, intensities and orientations, of a given image. I used open-source codes as a MATLAB toolbox (Walther & Koch, 2006) with default settings. Since apes made about 20 fixations during the 4 s presentation of each image (mean \pm SD = 18.7 ± 3.4), I calculated 20 predicted locations of fixations for each image used in experiments 1–4 using the model (Figure A2.1). I then counted the fixations that fell into the defined AOIs (adult or infant faces).

2.3 Results

2.3.1 Experiment 1 (conspecific images)

The ANOVA on the viewing time of the two species for conspecific adult and infant faces revealed a significant interaction between participant species and AOI ($F_{1, 19} = 5.56, P = 0.029, \eta^2_p = 0.23$; Figure 2.2). In addition, I found a nonsignificant trend in the main effect of participant species ($F_{1, 19} = 3.72, P = 0.069, \eta^2_p = 0.16$) and no significant main effect of AOI ($F_{1, 19} = 2.67, P = 0.12, \eta^2_p = 0.12$). The interaction effect can be explained by the chimpanzees viewing infant faces for longer than adult faces ($t_{14} = 3.67, P = 0.003, \text{Cohen's } d = 1.18$), whereas bonobos did not ($t_5 = 0.45, P = 0.67, \text{Cohen's } d = 0.19$). Moreover, bonobos viewed the faces of conspecific adults for longer than chimpanzees did ($t_{19} = 3.69, P = 0.002, \text{Cohen's } d = 1.58$), and the two species viewed the faces of conspecific infants for a similar duration ($t_{19} = 0.14, P = 0.89, \text{Cohen's } d = 0.066$). The effect of demographic factors other than species, such as age, sex, and visual and maternal experience, were visually inspected in Table A2.1 and Figure A 2.2 and A 2.3. I did not find any systematic individual differences, except for a potential sex difference in bonobos; the two male bonobos viewed the faces of adults for longer than those of infants, whereas females did not (Figure A 2.3).

2.3.2 Experiment 2 (heterospecific ape images)

The ANOVA on viewing time of heterospecific adult and infant faces revealed a significant interaction between participant species and AOI ($F_{1, 19} = 20.63, P < 0.001, \eta^2_p = 0.52$; Figure 2.2). In addition, I found significant main effects of participant species ($F_{1, 19} = 9.28, P = 0.007, \eta^2_p = 0.33$) and AOI ($F_{1, 19} = 16.70, P < 0.001, \eta^2_p = 0.47$). The interaction effect can be explained by the fact that bonobos viewed heterospecific adult faces for longer than chimpanzees did ($t_{19} = 4.31, P < 0.001, \text{Cohen's } d = 1.83$). Moreover, bonobos viewed the faces of chimpanzee adults for longer than those of chimpanzee infants ($t_5 = 4.67, P = 0.005, \text{Cohen's } d = 1.83$), whereas chimpanzees viewed the faces of

adult and infant bonobos for similar lengths of time ($t_{14} = 0.44$, $P = 0.67$, Cohen's $d = 0.10$). The two species viewed the faces of heterospecific infants for a similar duration ($t_{19} = 0.74$, $P = 0.47$, Cohen's $d = 0.44$). Visual inspection of the demographic factors other than species did not reveal any systematic individual differences (Table A 2.1, Figure A 2.2 and A 2.3).

2.3.3 Experiment 3 (outgroup monkey images)

The ANOVA on viewing time of adult and infant macaque faces revealed a significant interaction between participant species and AOI ($F_{1, 19} = 5.73$, $P = 0.027$, $\eta^2_p = 0.23$; Figure 2.2). I found no significant main effect of participant species ($F_{1, 19} = 0.026$, $P = 0.87$, $\eta^2_p = 0.001$) or AOI ($F_{1, 19} = 0.005$, $P = 0.94$, $\eta^2_p < 0.001$). The interaction effect can be explained by the fact that bonobos viewed the adult macaque faces for longer than the infant faces ($t_5 = 2.70$, $P = 0.042$, Cohen's $d = 0.89$), whereas chimpanzees viewed the faces of adult and infant macaques for a similar duration ($t_{14} = 1.94$, $P = 0.073$, Cohen's $d = 0.54$). Moreover, although not significant, bonobos tended to view the faces of adult macaques for longer than chimpanzees did ($t_{19} = 2.07$, $P = 0.052$, Cohen's $d = 0.97$), whereas the two species viewed the faces of outgroup infants for a similar duration ($t_{19} = 0.89$, $P = 0.38$, Cohen's $d = 0.58$). Visual inspection of the demographic factors other than species did not reveal any systematic individual differences (Table A2.1, Figure A2.2 and A2.3).

2.3.4 Experiment 4 (brightness-matched images)

When I matched the brightness of the infant and adult faces, chimpanzees did not distinguish between them ($t_{14} = -1.34$, $P = 0.20$, Cohen's $d = -0.40$; Figure 2.3). I then compared the results from this experiment with those from experiment 1 (with the original stimuli) using an ANOVA with experiment and AOI as the within-subject factors. I found a significant interaction effect between experiment and AOI ($F_{1, 14} = 18.95$, $P < 0.001$, $\eta^2_p = 0.58$). In addition, I found a significant main effect

of AOI ($F_{1, 14} = 8.18, P = 0.013, \eta^2_p = 0.37$) but not of experiment ($F_{1, 14} = 1.41, P = 0.25, \eta^2_p = 0.092$). The interaction effect can be explained by the fact that the chimpanzees viewed the brightness-matched infant faces for a shorter time than the original images ($t_{14} = 2.77, P = 0.015, \text{Cohen's } d = 0.62$), whereas they viewed the brightness-matched and original adult faces for a similar duration ($t_{14} = 1.90, P = 0.078, \text{Cohen's } d = 0.33$). This decrease in viewing time is unlikely to be due to fatigue or habituation across experiments, because I did not observe a general decrease in viewing time (i.e., no decrease in viewing time was observed for the adult faces). Visual inspection of the demographic factors other than species did not reveal any systematic individual differences (Table A 2.1, Figure A 2.2 and A 2.3).

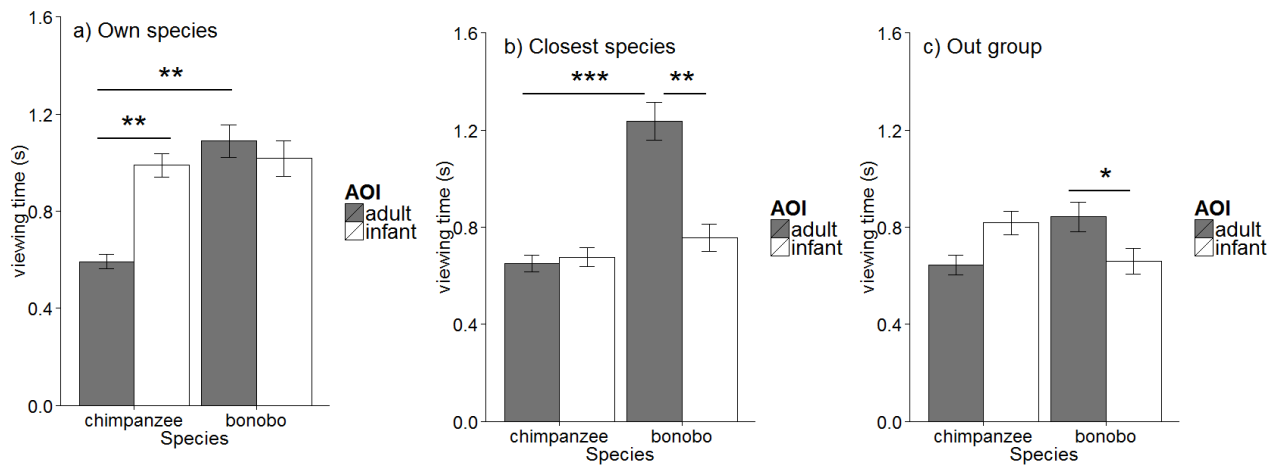


Figure 2.2. Mean viewing times of the areas of interest (AOI) of adult and infant faces by chimpanzees and bonobos in (a) experiment 1 (conspecific images), (b) experiment 2 (heterospecific ape images) and (c) experiment 3 (outgroup monkey images). * $P < 0.05$; ** $P < 0.01$; * $P < 0.001$.**

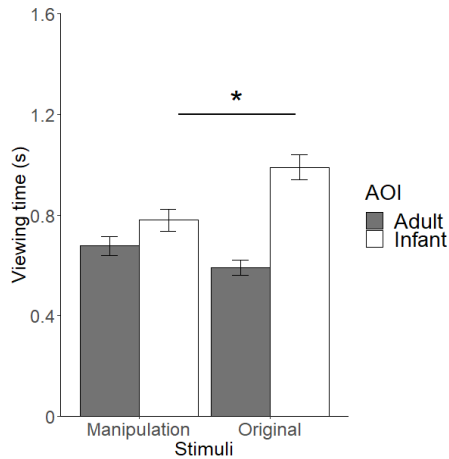


Figure 2.3. Mean viewing times of the areas of interest (AOI) of brightness-manipulated chimpanzee adult and infant faces by chimpanzees in experiment 4. Also shown (on the right) are the original data (from Experiment 1). * $P < 0.05$.

2.3.5 Saliency Analysis

The model predicted that adult and infant faces of the three species would receive the following mean number of fixations \pm SD (among 20 fixations): chimpanzee adult: 3.8 ± 3.07 (19 %); infant: 3 ± 1.86 (15%); bonobo adult: 2.95 ± 1.70 (14.8%); infant: 1.6 ± 1.50 (8%); Japanese macaque adult: 3.35 ± 1.46 (16.8%); infant: 1.8 ± 1.74 (9%); brightness-matched chimpanzee adult: 3.05 ± 2.82 (15.3%); infant: 2.4 ± 1.70 (12%). These results indicate that adult faces were predicted to receive more fixations than those of infants for all species presented, probably due to adults' larger face size in the images. However, infant chimpanzee faces were predicted to receive more fixations than those of bonobo and macaque infants, probably because of their higher contrasts (i.e., pale skin and dark coat). Importantly, these predicted patterns did not match the observed patterns for either participant species.

2.4 Discussions

This study tested whether bonobos and chimpanzees were attracted to the species-common

(e.g., a relatively large head and eyes) or a species-specific feature (conspicuous coloration) of conspecific and heterospecific infants in a full cross-species design. I found that chimpanzees, but not bonobos, were attracted to conspecific infants. A follow-up experiment in which facial coloration was matched between conspecific infants and adults indicated that chimpanzees were specifically attracted to the special infantile coloration of conspecific infants. I also discovered that neither chimpanzees nor bonobos were attracted to heterospecific macaque infants (with special infantile coloration). Interestingly, bonobos were more attracted to the images of heterospecific adults than those of heterospecific infants (both chimpanzee and macaque images). Overall, I confirmed that chimpanzees were most attracted to the infantile coloration of conspecific infants, and that bonobos did not seem to be attracted to any infantile feature of conspecifics and heterospecifics.

Two alternative explanations need to be ruled out. One is that chimpanzees and bonobos simply followed the prediction of the low-level model; namely, they viewed a face simply because of its brightness or size. However, the low-level model poorly matched the overall patterns of eye movement in both species. Importantly, although low-level perceptual features probably affect all species similarly, the results showed species-specific patterns of eye movement. Another alternative explanation is that novelty or rarity affected the observed patterns; for example, chimpanzees may have viewed conspecific infants for longer than adults just because the infants were novel or rare to them. However, this explanation is also unlikely because bonobos did not view conspecific infants in the same way as chimpanzees did. Additionally, all the ape participants, from two different facilities, had at least some experience of raising or interacting with conspecific infants. Moreover, differential experience of observing conspecific and heterospecific infants does not seem to explain the individual differences in the results (compare Figure A 2.2, A 2.3 and Table A 2.1).

My finding that chimpanzee adults were attracted to the special infantile coloration is consistent with previous observational studies of several species of monkeys (see Alley, 1980; Hrdy,

1976 for reviews), and also an experimental study with rhesus monkeys (Higley et al., 1987), but not with the results of Gerald et al. (2006). In addition to this finding, my study further revealed that chimpanzees were attracted only to conspecific infants and not to heterospecific infants that had special infantile coloration. Moreover, I found that bonobos were not attracted to any infantile features of conspecifics or heterospecifics. These results strongly suggest that attraction to infants is species specific in these ape species.

Bonobos clearly differed from chimpanzees in that they seemed to be equally attracted to conspecific infants and adults. Interestingly, bonobos viewed heterospecific adults for longer than heterospecific infants. One explanation for these results is that bonobos are generally more interested in adults than in infants. In addition, they might be interested in conspecific infants, to some extent, at least to a larger extent than heterospecific infants. The results might, thus, show that bonobos were equally attracted to conspecific adults and infants. The reason for this potential preference for adults is unclear. It is possible that, as this species is generally more tolerant than chimpanzees to outgroup individuals (Idani, 1990; Tan et al., 2017), they might not hesitate to gaze at adult faces. Alternatively, as this species generally prefers more dominant individuals (Krupenye & Hare, 2018), they might look more at individuals that appeared more dominant.

The observed differences between bonobos and chimpanzees support the hypothesis that the special infantile coloration of chimpanzees may have evolved as a strategy to reduce the risk of aggression, including infanticide, and to attract attention from conspecific adults. This hypothesis is also supported by previous reviews based on observational reports (Alley, 1980; Hrdy, 1976) but not species-wide surveys (Ross & Regan, 2000; Treves, 1997). However, my view is that special infantile coloration may induce changes in adult behaviors in subtle ways that cannot be captured in the survey data. Such changes may involve attracting adults' attention as I found in this study. Moreover, infantile coloration may also function as a releaser of behaviors, such as increased caregiving, increased tolerance and

inhibition of aggression. As previously noted, male chimpanzees tend to inhibit their aggression towards infants, while adults are less tolerant of juveniles, which are starting to lose their infantile features (van Lawick-Goodall, 1968). It remains an open question as to whether these infantile features increase the affective states of conspecific adults in chimpanzees.

The results did not support the prediction that bonobos and chimpanzees are attracted to the species-common baby schema, as humans typically are. This result might differ from that obtained by Sato et al. (2012), who found that Campbell's monkeys were attracted to the infants of heterospecific Japanese macaques. However, as noted earlier, because this previous study did not adopt a full cross-species design, it is currently unclear how its results can be compared with the present results. Thus, I have no evidence that primate or non-primate species possess heterospecific infant preferences similar to that of humans. This lack of evidence might be attributed to the lack of systematic experiments with a wide variety of species, rather than the absence of such preferences which may exist in some species. A good starting point in this search might be to test the species reported to adopt distantly related species (e.g., capuchins; Izar et al., 2006).

The results also suggest that a preference for the species-common baby schema is unique to humans, at least when compared with the two closely related species, bonobos and chimpanzees. Such preferences might be limited to certain populations of humans, because previous studies have focused, almost exclusively, on people in developed countries. That is, it is possible that preference for heterospecific infants has only arisen in recent history, and in countries with a specific cultural background (e.g., exposed to companion animals or cartoon characters with exaggerated baby schema). However, if a preference for heterospecific infants is a derived trait in humans, it might be a by-product of alloparenting, that is, an over-generalization of strong responses to various infantile features, including baby schema. Humans did not acquire species-specific infantile traits, in contrast to chimpanzees. However, because human infants are altricial and require extensive care from both related

and unrelated adults (even more so than bonobos and chimpanzees), humans might have acquired especially strong affiliative responses to infants with strong baby schema, which might be generalized to heterospecific infants with the same baby schema. If the preference of humans for heterospecific infants has an evolutionary origin, such preferences might have promoted the domestication of heterospecific species, such as dogs and cats, because domestication tends to promote the evolution of infant-like features in animals (e.g., Frank & Frank, 1982). The preference of humans for heterospecific infants is not limited to domesticated species, however. Sanefuji et al. (2007) showed that both adults and children prefer the infants of both familiar/pet animals (e.g., dogs and cats) and unfamiliar/nonpet animals (e.g., chimpanzees). Further comparative and cross-cultural studies would be beneficial to address these remaining questions.

In conclusion, I have shown that chimpanzees, but not bonobos, paid more attention to infant than adult conspecifics. They seemed to be particularly attracted to the special infantile coloration of conspecific infants. The observed differences between the species may be related to their unique socioecological styles. Neither species was particularly attracted to the species-common infantile features. These results strongly suggest that preference for infants is species-specific in these ape species, in contrast to the view that nonhuman animals also have a general preference for species-common infantile features. Therefore, to obtain a more complete comparative picture, a wider variety of species with and without special infantile features should be tested using a full cross-species design.

2.5 Appendix

The experts who estimated the approximate age of depicted infants had at least several years of experience in research or care taking on each species. I used forced choice tests but if the experts reported two adjacent values for a certain image, I took the median of the two values for that image. Nine chimpanzee experts, and five bonobo and Japanese macaque experts each participated. I excluded the result of one additional chimpanzee expert because of experimenter error. For the chimpanzee images, the median value for each stimulus ranged between 1 and 5, with an overall estimated median (first–third quartile) age class of 3 (2.75–4), that is, 1–2 years old. For the bonobo images, the median value for each stimulus ranged between 1 and 5, with an overall estimated median (first–third quartile) age class of 3 (2–3.63), that is, also 1–2 years old. For macaque images, the median value for each stimulus ranged between 1 and 3, and the overall estimated median (first–third quartile) age class was 1 (1–2), that is, 0–0.5 years old. Intraclass correlation coefficients (ICC, single measures) were 0.72, 0.69 and 0.61 for the chimpanzee, bonobo and macaque images, respectively. The relatively low ICC for macaque images was probably obtained because of the difficulty in distinguishing between age classes (1) 0–0.5 years old and (2) 0.5–1 years old.

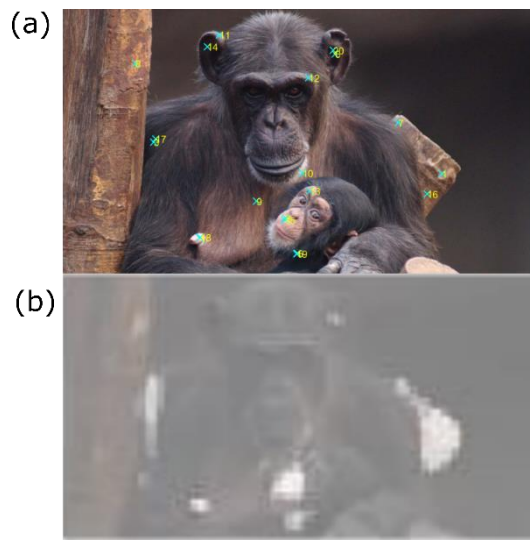


Figure A2.1. An example result from the saliency model. (a) The fixation locations predicted by the saliency model. (b) The predicted saliency map (brighter spots indicate more salient pixels).

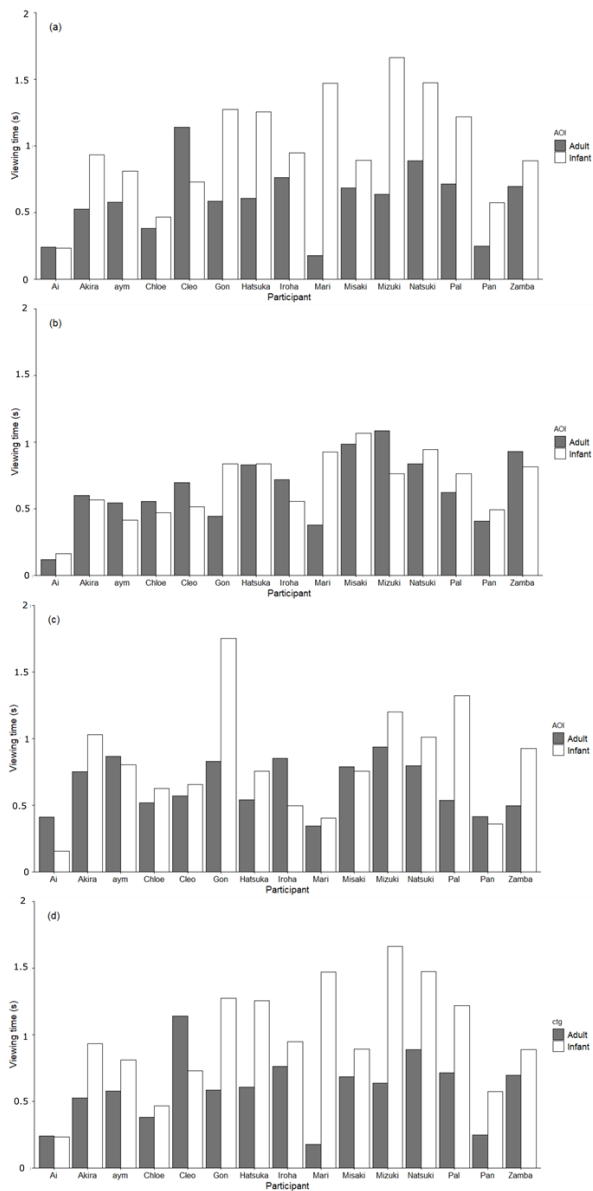


Figure A2.2. Individual viewing times of the areas of interest (AOI) of adult and infant faces for chimpanzees in experiments 1–3 with (a) conspecific images, (b) heterospecific ape images and (c) outgroup monkey images and (d) brightness-manipulated chimpanzee images.

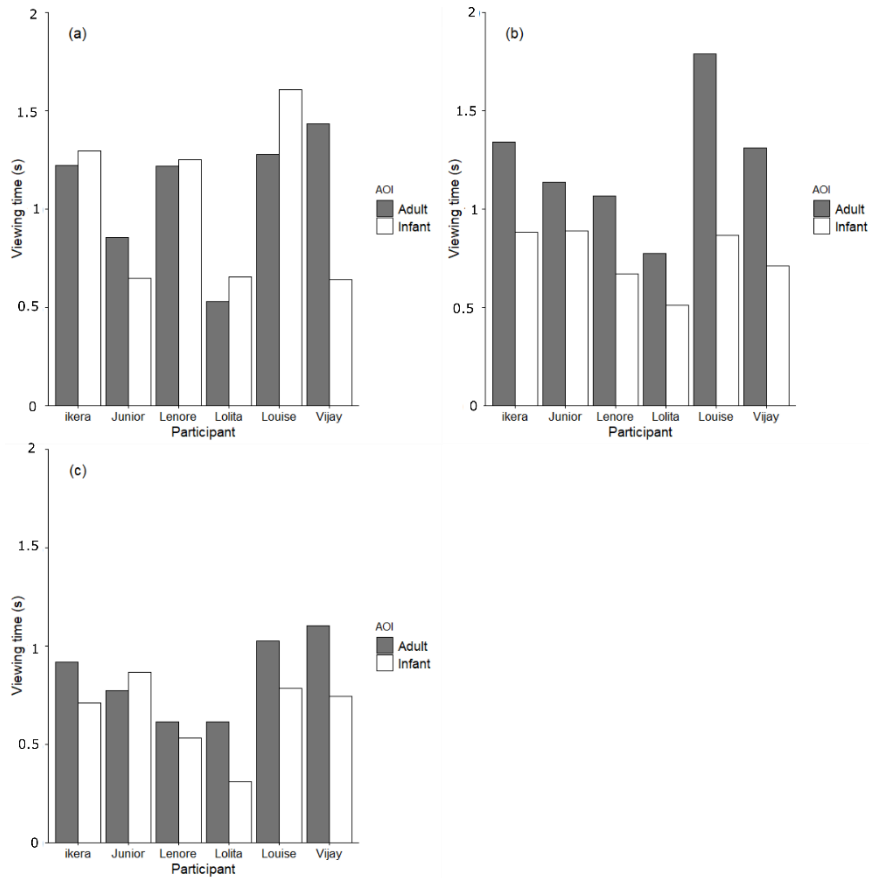


Figure A2.3. Individual viewing times of the areas of interest (AOI) of adult and infant faces for bonobos in experiments 1–4 with (a) conspecific images, (b) heterospecific ape images, (c) outgroup monkey images.

Table A 2.1. Participant information

Individual name (GAIN ¹ ID)	Sex	Facility	Age	Birth experience
Chimpanzee				
Ai (0434)	female	PRI	41	parous
Akira (0435)	male	PRI	41	-
Ayumu (0608)	male	PRI	17	-
Chloe (0441)	female	PRI	36	parous
Cleo (0609)	female	PRI	17	nulliparous
Gon (0437)	male	PRI	51	-
Hatsuka (0704)	female	KS	9	nulliparous
Iroha (0708)	female	KS	9	nulliparous
Mari (0274)	female	PRI	41	parous
Misaki (0593)	female	KS	18	parous
Mizuki (0559)	female	KS	20	parous
Natsuki (0677)	female	KS	12	nulliparous
Pal (0611)	female	PRI	17	nulliparous
Pan (0440)	female	PRI	33	parous
Zamba (0543)	male	KS	22	-
Bonobo				
Connie Lenore (0006)	female	KS	35	parous
Ikeru (0008)	female	KS	25	parous
Junior (0009)	male	KS	22	-
Lolita (0007)	female	KS	28	parous
Louise (0010)	female	KS	45	parous
Vijay (0011)	male	KS	13	-

KS chimpanzees had occasional visual access to KS bonobos, and vice versa. Neither species had visual access to macaques. PRI chimpanzees had daily visual access to rhesus macaques including both adults and infants but had no visual access to bonobos.

¹GAIN (Great Ape Information Network) is the information network for Hominoidea living in Japan.

Chapter 3: Oxytocin Administration Effect on Visual Preference to Infants in Chimpanzees

3.1 Introduction

Care by adults is critical for mammalian infants. Previous studies in humans have revealed the various cognitive mechanisms that are likely to support infant care, such as preference or attentional bias for infant faces. For example, infant faces attract attention compared with adult faces (for review Lucion et al., 2017). Behavioral studies have shown that infant faces have incentive salience (e.g., Alley, 1981; Glocker, Langleben, Ruparel, Loughhead, Gur, et al., 2009; Hildebrandt & Fitzgerald, 1979; Sternglanz et al., 1977). Moreover, the evidence of rewarding value of infant faces is supported by neuroscientific studies. Infant faces, but not adult faces, activate the medial orbitofrontal cortex, which is implicated in reward perception (Kringelbach et al., 2008). Exaggeration of infantile facial features activates the nucleus accumbens, which are also known for mediating reward processing (Glocker, Langleben, Ruparel, Loughhead, Valdez, et al., 2009). These findings indicate that humans have attentional bias for infant faces and perceive an infant face as rewarding. These induce and maintain parenting behavior. Given that infant care is conserved behavior among primates, our evolutionary relatives, apes, may also have attentional bias for infant faces and perceive them as rewarding stimuli.

Chapter 2 revealed that chimpanzees show visual preference to conspecific infants. I recorded chimpanzees' and bonobos' eye movements through an eye-tracker while they looked at images of conspecific mothers and infants. The results of the analysis found that chimpanzees looked at conspecific infant faces longer than adult ones, while bonobos did not show such visual preference. However, bonobos did not look at adult and infant conspecific faces for different durations. Although chimpanzee infants have conspicuous face coloration, a low-level saliency analysis indicated that chimpanzees' visual preference for infant faces are not only because of saliency. However, it does not

permit us to draw conclusions on whether apes' visual preference for conspecific infants is regulated by parenting or affiliative motivation. Interpreting visual preference requires caution, since the preference is "implicit and based on an inference (Damon et al., 2019, p. 268)." When given two visual stimuli, the level of interest, as well as or even more than the level of pleasant feeling, determines visual "preference" (Humphrey, 1972). Moreover, chimpanzees are known to commit infanticide (M. L. Wilson et al., 2014). Therefore, chimpanzee's visual attention to infants may not necessarily reflect "preference" or affiliative motivation, but it may reflect agonistic motivation.

One way to interpret apes' visual preference may be to investigate the interaction between the visual attention to infants and a hormone known to be involved in the regulation of parenting behavior. Oxytocin (OT) is a neuropeptide hormone that mediates complex social behaviors, especially parenting, across mammals. In both humans and non-humans, OT is important in the emergence and maintenance of mother-infant bonds (for review Nagasawa et al., 2012; Scatliffe et al., 2019). Positive correlations between endogenous OT level, and parenting motivation and behavior are repeatedly reported. After reviewing 17 studies in humans, Scatliffe et al., (2019) concluded the important role of OT in attachment between infants and parents. During infant-parent interaction, OT levels increased in infants, mothers, and fathers; parents with higher OT levels show more synchrony and responsiveness in the interaction with their infants. It is also reported that a mother's OT levels early in pregnancy and during the postpartum period were correlated with maternal bonding behavior such as gaze and affectionate touch to infants (Feldman et al., 2007). Besides those correlational studies, recent research has been directly examining the role of OT by enhancing the level through OT administration. For example, Marsh et al., (2012) tested the effect of intranasal OT administration on preference for infant faces. The participants were asked to rate the attractiveness of adult and infant faces after administration of either OT or placebo. They found that infant faces were preferred more after OT administration compared with placebo administration. Another study tested the influence of intranasally administered OT on functional brain

connectivity in response to infant laughter by using functional magnetic resonance imaging (fMRI) (Riem et al., 2012). OT administration enhanced the functional connectivity between the amygdala and regions involved in emotion regulation during infant laughter. They concluded that OT administration might reduce negative emotional arousal while increasing the incentive salience of infant laughter.

There are some attempts to examine the relationship between OT and parenting behavior in non-human primates. The findings in non-human primates do not conflict with the previous human studies. Maestriperi et al., (2009) investigated the relationship between maternal behavior and physiology in free-ranging rhesus macaques. They found a positive correlation between nursing and grooming behavior and maternal OT levels. The role of OT in care-giving behaviors has been examined in bonobos. Boose et al., (2018) tested the relationship between infant handling behavior and urinary OT in captive bonobos. They found that the post-handling OT levels were higher than the baseline level in adolescent and juvenile females, but lower in all other age-sex categories. Few studies examined the exogenous OT effect on parenting behavior in non-human primates. Saito & Nakamura (2011) tested the effect of OT administration on paternal behavior in common marmosets. They found that OT reduced the frequency of a father's refusal of food transfer to the offspring. This evidence demonstrates that OT is key to mediating parenting behavior in both humans and non-human primates.

Furthermore, OT plays multifunctional roles beyond regulating parenting behavior in the social domain. OT administration influences various components of the social dimension, including social memory, emotion recognition, empathy, trust behavior, and in-group/out-group recognition. These various outcomes can be explained by three (not mutually exclusive) mechanisms: *affiliative motivation*, *anxiety reduction*, and *social salience* (Bartz et al., 2011). According to the affiliative motivation hypothesis, OT facilitates motivational states related to affiliation. This hypothesis is consistent with the evidence in animals, where OT strengthens the formation of the social bond, including mother-infant bonds and pair bonds in monogamous species (Lim & Young, 2006). According to the anxiety reduction

hypothesis, OT affects social recognition performance by attenuating social anxiety (e.g., MacDonald & MacDonald, 2010). For example, this hypothesis accounts for the outcome when OT administration increases the performance of gazing into another's eyes in people with autism spectrum disorder, who typically have difficulty responding appropriately to social cues (Guastella et al., 2010). Lastly, the social-salience hypothesis proposes that OT increases the salience of social cues (e.g., Olf et al., 2013; Shamay-Tsoory & Abu-Akel, 2016). According to this hypothesis, OT administration increases the salience of social cues, and it results in either positive (i.e., social) or negative (i.e., antisocial) effects depending on the context and interindividual factors.

Recently, studies have examined intranasal OT administration in a broader context beyond humans, including non-human primates such as capuchin monkeys (Brosnan et al., 2015), macaques (Ebitz et al., 2013; Jiang & Platt, 2018b, 2018a; Parr et al., 2013; Putnam et al., 2016; Simpson et al., 2014, 2017; Zarei et al., 2019), and apes (Brooks et al., 2021; Hall et al., 2019; Proctor et al., 2016). Although few studies investigated the effect of OT on parenting behavior, the validity of intranasal OT administration on non-human primates is confirmed. Parr et al., (2013) administered OT to rhesus macaques and tested how the effects on attention to emotional stimuli. They reported that OT administration significantly reduced monkeys' attention to negative facial expressions, but not neutral faces or non-social stimuli, which suggests OT's function to reduce aversiveness of social stimuli as reported in humans. As a more relevant work, Brooks et al. (2021) recently tested the influence of OT administration on eye-contact in chimpanzees and bonobos and found the differential effect of OT between the two species. They reported that enhanced OT increased looking duration to eyes in bonobos, while it affected chimpanzees' gaze conversely. Original visual attention to eyes differs between the two species; bonobos look at conspecific eyes more than chimpanzees do (F. Kano et al., 2015). Thus, Brooks et al. (2021) concluded that OT administration may enhance apes' species-specific behavioral tendencies based on the social saliency hypothesis.

In this study, I administered OT or a placebo to chimpanzees and bonobos and measured the looking time at adult and infant faces to determine how the administration changes visual interest to infant conspecifics. The method of eye-tracking, including stimuli, followed and modified my previous study (Chapter 2). The method of nasal administration of OT and placebo followed the previous study, which administered OT to both chimpanzees and bonobos (Brooks et al., 2021). I predicted possible outcomes. First, I hypothesized that if apes' looking behavior at infants in our previous study originated from their affective motivation of nurturance, enhanced OT would prolong looking time at infants. Second, if their visual preference for infants comes from an agonistic motivation related with infanticide, their looking time at infant images would decrease through OT administration. This is because OT functions counter to testosterone (Holtfrerich et al., 2016; Winslow & Insel, 1991), which is associated with aggression (Book et al., 2001). Indeed, in rodents, administration of OT inhibited infanticide (McCarthy, 1990), while administration of testosterone facilitated infanticide in female mice (Gandelman & Saal, 1975). These two predictions were based on the affiliative motivation hypothesis. Based on other hypotheses, if the motivation of looking at infants is neither parental nor infanticidal but something else (e.g., reflecting an avoidance to gazing at conspecific adults), I predicted other outcomes. Third prediction is that OT administration would increase the looking time at faces in general, especially adult faces, in both species based on anxiety reduction hypothesis. If the gaze to face including eyes is somehow threatening for apes, it may be facilitated by attenuating anxiety. The last prediction is the one based on the social-salience hypothesis. The social-salience hypothesis assumes that OT enhances pre-existing social sensitivities (Shamay-Tsoory & Abu-Akel, 2016). The differential outcomes of OT administration between chimpanzees and bonobos on social interest in the previous study (Brooks et al., 2021) can also be explained by this social-salience hypothesis. The results of Chapter 2 suggest that chimpanzees, but not bonobos, originally have looking bias for infants. Therefore, the fourth prediction is that the looking time at infants in chimpanzees, but not bonobos, would be increased by OT

administration based on the social salience hypothesis.

3.2 Methods

3.2.1 Participants

Sixteen chimpanzees (*Pan troglodytes verus*) and five bonobos (*Pan paniscus*) participated in the experiments (Table 3). The participants included three male chimpanzees and one male bonobo. Ten chimpanzees live in the Primate Research Institute (PRI), all bonobos and six chimpanzees live in Kumamoto Sanctuary (KS). All primates, except Pendesa, attended the previous eye-tracking experiment (Chapter 2). Apes were living in an enriched environment with an outdoor compound and vegetation attached to indoor enclosures. Participants were neither food- nor water-deprived, and they lived in social groups. They receive food (fresh fruits, vegetables, sweet potatoes, and nutritionally balanced biscuits) several times each day and have constant access to water. All procedures adhered to institutional guidelines (Primate Research Institute 2010 version of “The Guidelines for the Care and Use of Laboratory Primates”). The experimental design was approved by the Animal Welfare and Animal Care Committee of the PRI (2020-207), the Ethics Committee of the Wildlife Research Center (WRC-2019-KS014A), and the Animal Research Committee of Kyoto University.

3.2.2 Stimuli

I prepared 10 images for each of the four stimuli sets; hence, 40 images in total for chimpanzees and bonobos. Among them, two stimuli sets (e.g., A-1, A-2) were for the OT condition, and the other two (e.g., B-1, B-2) for the saline condition. For half of the participants stimuli of set A was presented in OT condition and those of set B were presented in saline condition, and vice versa for the other participants. A mother-infant pair who are unfamiliar to the participants was depicted with a naturalistic background for each stimuli set (Figure 3.1). The images were taken by the authors, provided

by colleagues, or taken from public sources, and were trimmed in Adobe Photoshop Elements 15. I presented the same image only once for the same individual among conditions to avoid the habituation effect caused by repetition. Half of the stimuli in each set were used in the previous study (Chapter 2), approximately two years prior. The other half the stimuli images (n=20) were selected with the same criteria for this study.

3.2.3 Apparatus and Procedure

Each individual received two OT sessions and two saline sessions. Only one session was conducted per day for each individual. I set at least four days between each session to avoid any possible influence of the previous session. Reception of OT or saline on the day was predetermined. Half of the participants experienced the OT-Saline-Saline-OT order, while the other half experienced the Saline-OT-OT-Saline order. The participants were called as daily experiments, and their participation was voluntary. Further, they could stop the experiment whenever they wanted. The participants were not physically restrained during the experimental procedures.

OT and saline administration

The methods of administration, including the dose of OT (i.e., 40 IU), followed the previous study of OT administration in apes (Brooks et al., 2021). When a participant entered the experimental booth, I administered either OT or saline with a nebulizer (Figure 3.1, NE-U22-4, Omron, Kyoto, Japan) through a custom-made box that was sized to the ape's head (13 w × 16.5 h × 8 d cm) and attached to the experimental booth. I used the box so that the nebulized mist was kept near the nose of the participants. The total administration duration was 4 min. I used a timer to measure the administration time and stopped it whenever the participant moved their nose away from the nebulizer. I used a concentration of 40 IU/mL of OT. The mist was nebulized at a rate of 0.25 ml/min so that about 40 IU

of OT were administered for 4 min cumulatively. During the administration, the participants could sip diluted juice to keep them motivated and to keep their head movement minimized. After the administration, the participants spent 30 min either doing irrelevant cognitive tasks that did not include social stimuli or took a rest, depending on the preference of the participant. The manner spending time was consistent for each individual. To keep them calm during the wait, the participants received pieces of fruits, but social interaction was avoided as much as possible.

Eye tracking task

For recording eye gaze, an infrared head-free Tobii eye tracker (60 Hz; X300; Tobii Technology AB, Stockholm, Sweden) was used. Each stimuli set was presented at a resolution of 1,280 x 720 pixels on a 23-inch LCD monitor using Tobii Studio software (version 3.2.1). The eye tracker and monitor were placed outside the experimental booth at around 70 cm viewing distance through an acrylic panel. During the eye tracking, the participant could sip juice to minimize head movement. Calibration was conducted by presenting two images at the corner of the monitor before testing each participant. I visually checked the calibration accuracy each time by monitoring their gaze to some reference points before testing and conducted calibration again if necessary. In one session, 10 images were presented. The order of the image was counterbalanced among individuals. Each image was presented for 4 sec. Before each image, the fixation cross was briefly (0.5 sec) appeared at the center of the monitor. For another study, PRI chimpanzee participants were presented with a series of conspecific adult face stimuli before my stimuli set.



Figure 3.1 A) Example of the presented stimuli. B) OT administration with a nebulizer.

3.2.4 Analysis

Areas of interest (AOIs) were defined for each stimulus and included faces of an adult and an infant. AOIs were defined slightly bigger than actual faces to accommodate possible fixation errors. Adult faces in the stimuli were usually bigger than infant faces since I used natural images with minimum manipulation, but I did not correct the data based on size difference of AOI, following my previous study in Chapter 2. The looking time for each AOI was analyzed with Tobii Studio software (version 3.2.1).

The looking time at adult or infant faces for each stimuli was analyzed by a generalized linear mixed model (GLMM). I used R 3.6.2. (R Core Team, 2018) with the “lme4” package (Bates et al., 2015, p. 4). For GLMM analysis, the looking time at adult faces was included as response variables, and the condition (OT or saline), species (chimpanzees or bonobos), interaction of them, and session order (1-4, the variable was standardized) were included as explanatory variables. The participant ID (as random slope) and stimuli (as random intercept) were also included. For chimpanzees, the participant ID was nested in a participant group (KS or PRI). I used a gamma distribution. The looking time at infant faces was analyzed in the same way. In addition, the total frequency of the first look for each session was analyzed with the same GLMM analysis but with a binomial distribution. The first look was defined as either an adult or infant face, with shorter latency to look (only latency longer than 200 ms

were considered), and coded either 0 (adult) or 1 (infant).

3.3 Results

Figure 3.2 shows the average looking time at adult and infant faces for each condition in chimpanzees and bonobos. Analysis of the looking time at faces found significant effect of species on the looking time at adult faces (Estimate = 0.53, SE = 0.25, $t = 2.11$, $p = .03$, see Table A3.1), which indicates that bonobos looked at adult faces longer than chimpanzees did. However, there was no significant effect of any other factors: main effect of condition (adult: Estimate = 0.003, SE = 0.27, $t = 0.01$, $p = .99$, infant: Estimate = -0.07, SE = 0.27, $t = -0.28$, $p = .78$), species (infant: Estimate = 0.14, SE = 0.23, $t = 0.60$, $p = .55$), and the interaction between them (adult: Estimate = -0.18, SE = 0.35, $t = -0.50$, $p = .61$, infant: Estimate = 0.01, SE = 0.32, $t = 0.04$, $p = .97$). Figure 3.3 shows the average differential score, subtracting the total adult looking time from the total infant looking time during each session and dividing by the sum for each session (see also Figure A 3.1). Visual inspection found no sex difference (Figure 3.3 and Figure A 3.1) and analyzing only female data did not affect the results. As additional data, the average looking time at each facial part of adult and infant faces is illustrated in Figure A 3.2.

I also analyzed the first look: whether the participant looked at the adult or infant face first for each stimulus. Analysis of the first look found significant effect of species (Estimate = 0.91, SE = 0.42, $Z = 2.18$, $p = .03$), indicating that the first look was more likely to be infant faces in chimpanzees than in bonobos; but there was no significant effect of condition (Estimate = 0.21, SE = 0.33, $Z = 0.64$, $p = .52$) and the interaction between them (Estimate = -0.51, SE = 0.40, $Z = -1.27$, $p = .20$).

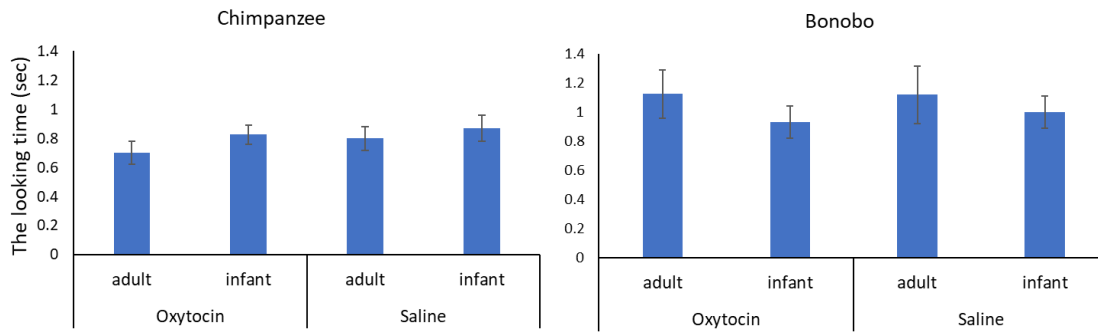


Figure 3.2. Average looking time at adult and infant faces in chimpanzees and bonobos. Error bar indicates standard error.

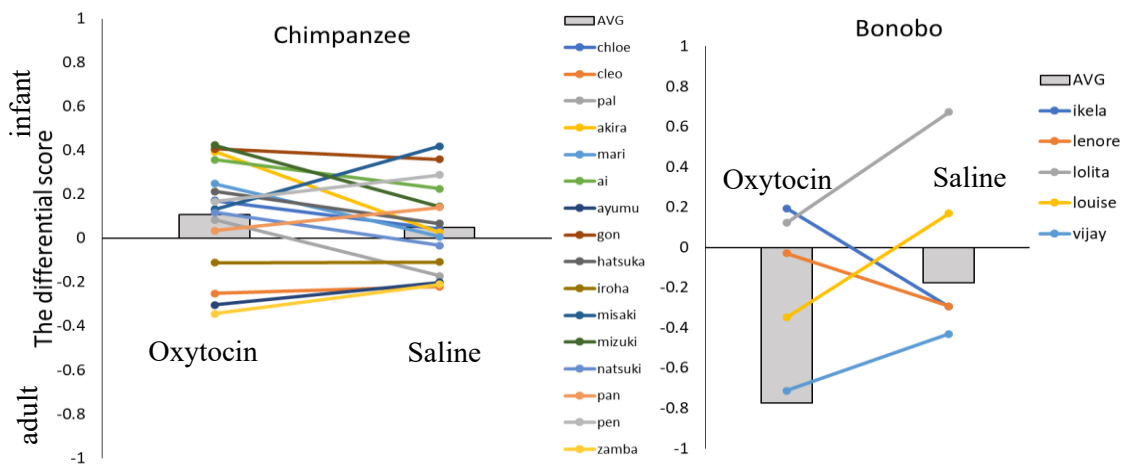


Figure 3.3. Differential score for each condition in chimpanzees and bonobos. A positive value indicates the looking time at infants was greater than to the looking time at adults.

3.4 Discussions

This chapter investigated the effect of OT administration on apes' looking pattern at adult and infant faces to understand the motivation regulating visual preference for infants. The results indicate an absence of the effect of OT administration; therefore, it remains unclear which of the four predictions was supported. This may indicate that enhanced exogenous OT does not have robust and consistent influence on apes' visual attention for adult and infant conspecifics. However, it is also possible that the administration effect may have been masked by other factors, including potential artifacts or individual

differences discussed below. Further study should be conducted before making a conclusion.

In both species, the individual differences of the OT effect on the interest for infants was quite large (Figure 3.3). Since the sample size was not large, especially for bonobo participants, such individual differences could have masked the effect of administration, if any. This is not surprising given that the conditional and differential effect of OT administration is commonly reported in both humans and non-humans (e.g., Bartz et al., 2011). For example, gender difference of the effect of OT is reported in many human studies (Feng et al., 2015; Rilling et al., 2014; Wang et al., 2013; Wigton et al., 2015). Such effect of gender on OT administration is also reported in non-human primates. Simpson et al., (2017) tested the effect of OT administration on social cognitive skills (i.e., working memory and gaze following) in infant rhesus macaques and found that OT improved these in females but not in males. Moreover, Marsh et al., (2012) found individual differences in humans based on genotype of the effect of OT; the enhanced preference of infant faces by OT was observed only in participants homozygous for the rs53576G allele. Additionally, Holtfrerich et al. (2016) found that OT administration decreased response time to faces (both infants and adults) in target detection tasks, but only in women whose endogenous testosterone was high. Investigating the effect of OT administration and caregiving motivation on neural response to infant faces demonstrated that participants with high caregiving motivation are susceptible to the effect of OT administration (Bos et al., 2018). Thus, these factors may have affected the results in the present study. Unfortunately, however, it is difficult to confirm the critical factor to explain the individual difference in the effect of OT. Future study should investigate how individual factors, such as gender, age, and motivational difference, affect the OT effect on attention to infants in non-human primates.

One limitation of this study is that I could not control the baseline looking time difference among stimuli. To prevent the habituation effect, the stimuli set was presented only once across the sessions. This makes the comparison of the looking time for the same stimuli set between two

administration conditions within participants impossible. The baseline interest to each stimulus differs among participants and it may have overridden the effect of administration condition. Future studies should modify the experimental design and present the same stimuli set between OT and placebo conditions within participants. It was unexpected that chimpanzees' infant looking bias observed in Chapter 2 was not clear in the baseline (i.e., saline) condition in this study. The different results between the previous study and this study might come from the different stimuli or experimental design used (i.e., administration and 30 min waiting period before eye-tacking). Another limitation of this study is that validation of intranasal OT administration by hormonal measurement was not conducted. However, a previous study with rhesus macaques confirmed increased concentrations of OT in cerebrospinal fluid by aerosolized OT administration (Modi, 2014). Moreover, the change of looking pattern by OT administration was reported in a previous study (Brooks et al., 2021) testing apes, including the current participants. I adopted the exact same method of administration as the previous study did. Therefore, the possibility that the procedure of administration was inappropriate is unlikely, although it cannot be denied completely.

It may be worth trying to test the effect of OT administration on apes' visual interest to emotional stimuli of adults and infants. Parental caregiving motivation is supposed to be regulated by two distinct factors: *protection* and *nurturance* (Hofer et al., 2018). Protection refers to the motivation to protect infants from danger, while nurturance reflects a tendency to treat infants in a supportive way and is related to rewarding recognition of infant cuteness. These two aspects of parenting behavior are supposed to be conserved. For example, female rodents show two distinct corresponding types of parental care, namely maternal aggression and maternal care (Bosch & Neumann, 2012). It may be possible that OT influences protection or maternal aggression, rather than nurturance or maternal care. Although some studies reported the significant effect of OT for positive or neutral infant stimuli (Marsh et al., 2012; Riem et al., 2012), Gregory et al. (2015) found that intranasal OT administration enhanced

ventral tegmental area (VTA) activation for crying infants but not for smiling infants. Thus, it is possible that OT administration may have a more robust impact for negative rather than positive infant stimuli. Studies should investigate whether OT administration in apes has a different influence on the protection and nurturance aspect of parenting behavior by using negative stimuli as well as positive or neutral stimuli as used in the current study.

3.5 Table

Table A 3.1. Participant information

Individual name (GAIN ¹ ID)	Sex	Facility	Age	Birth experience
Chimpanzee				
Ai (0434)	female	PRI	43	parous
Akira (0435)	male	PRI	43	-
Ayumu (0608)	male	PRI	19	-
Chloe (0441)	female	PRI	39	parous
Cleo (0609)	female	PRI	19	nulliparous
Gon (0437)	male	PRI	53	-
Mari (0274)	female	PRI	43	parous
Pal (0611)	female	PRI	19	nulliparous
Pan (0440)	female	PRI	36	parous
Pendesa (0095)	female	PRI	43	nulliparous
Hatsuka (0704)	female	KS	12	nulliparous
Iroha (0708)	female	KS	12	nulliparous
Misaki (0593)	female	KS	21	parous
Mizuki (0559)	female	KS	23	nulliparous
Natsuki (0677)	female	KS	15	nulliparous
Zamba (0543)	male	KS	22	-
Bonobo				
Connie Lenore (0006)	female	KS	38	parous
Ikeru (0008)	female	KS	28	parous
Lolita (0007)	female	KS	31	parous
Louise (0010)	female	KS	47	parous
Vijay (0011)	male	KS	16	-

¹GAIN (Great Ape Information Network) is the information network for Hominoidea living in Japan.

3.6 Appendix

Table A 3.1. the results of GLMM analysis

Looking time		Estimate	SE	<i>t</i>	<i>p</i>	95 % CI
Adult face	Intercept	0.89	0.19	4.73	<.001	[0.52, 1.26]
	Species*Condition	-0.18	0.35	-0.50	.61	[-0.86,0.50]
	Species	0.53	0.25	2.11	.03	[0.04,1.03]
	Condition	0.003	0.27	0.01	.99	[-0.52,0.53]
Infant Face	Intercept	1.08	0.19	5.52	<.001	[0.69,1.46]
	Species*Condition	0.01	0.32	0.04	.97	[-0.61,0.63]
	Species	0.14	0.23	0.60	.55	[-0.31,0.59]
	Condition	-0.07	0.27	-0.28	.78	[-0.60,0.45]
First look		Estimate	SE	<i>Z</i>	<i>p</i>	95 % CI
	Intercept	-0.30	0.35	-0.86	.39	[-1.0,0.39]
	Species*Condition	-0.51	0.40	-1.27	.20	[-1.30,0.28]
	Species	0.91	0.42	2.18	.03	[0.09,1.73]
	Condition	0.21	0.33	0.64	.52	[-0.44,0.86]

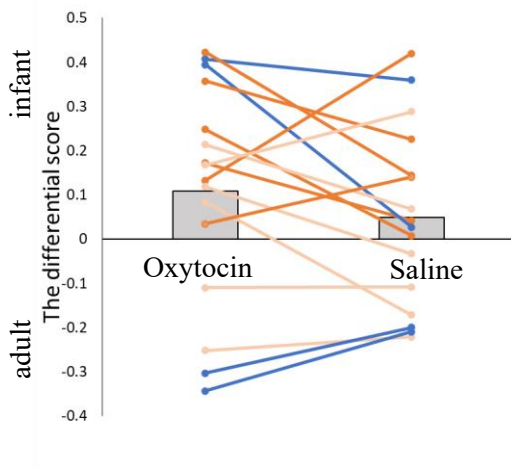


Figure A3.1. Differential score for each participant sex in chimpanzees. A positive value indicates the looking time at infants was greater than the looking time at adults. The graph represents the same results as Figure 3.2 with the blue line indicating a male, the pale pink line indicating a nulliparous female, and the orange line indicating a parous female.

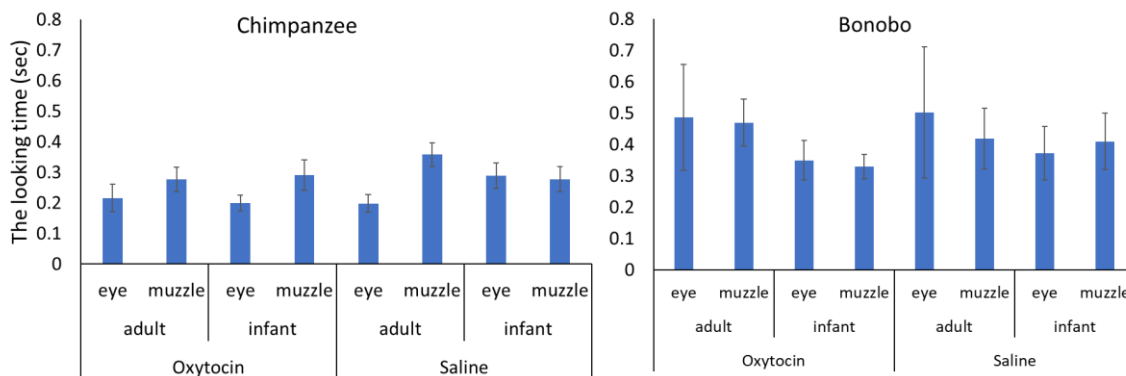


Figure A3. 2. Looking time at facial parts (i.e., eyes and a muzzle) for each condition in chimpanzees and bonobos.

Chapter 4: Color Matters More than Shape for Chimpanzees' Recognition of Developmental Face Changes

This chapter was published in the journal: Kawaguchi, Nakamura & Tomonaga (2020)

Scientific Reports, 10, doi: 10.1038/s41598-020-75284-2.

4.1 Introduction

Faces are a rich source of biological and social information such as age, identity, gender, emotional states, impressions and so on in humans (Bruce & Young, 2012; G. Rhodes et al., 2011). The ability to extract various information from faces plays a critical role in a wide range of social and emotional interactions. Comparative cognitive studies have investigated the role of face perception across species in order to reveal the evolutionary origins of face perception in humans. Thus, non-human primates are a good target because of their phylogenetic closeness to humans. Most non-human primates have trichromacy like humans, which is supposed to benefit them for detecting variations in facial coloration indicating such as emotional, breeding, or health status (Changizi et al., 2006; Hiramatsu et al., 2017; H. M. Rowland & Burriss, 2017; Thorstenson, 2018). Indeed, non-human primates are able to extract different types of information from faces (Leopold & Rhodes, 2010), including facial identity (Parr et al., 2000), facial expressions (Kanazawa, 1996; Parr, 2003), sex of the face (Koba et al., 2009), and so on, partially due to high sensitivity to facial coloration.

Among various social traits, age perception is a vitally important facial attribute because this particular cue helps animals behave appropriately toward other animals (Berry & McArthur, 1986). Animals should not treat an adult animal like an infant and vice versa. For example, adult animals should avoid immature animals as a mating partner; unfamiliar individuals can be a threat if s/he is an adult but

probably not if s/he is an infant. Although non-human animals can use various physical cues when judging age, including body size, body movement and vocalization, one prominent facial cue to age perception is baby schema (*Kindchenschema*) (Lorenz, 1943). Baby schema is a set of morphological features that are characteristic of infant appearance such as larger eyes relative to head size, a high and protruding forehead, and a smaller nose and mouth (Lorenz, 1943). Studies have shown that the baby schema makes human faces appear cuter and enhances viewers' caretaking motivations (Alley, 1981, 1983a, 1983b; Borgi et al., 2014; Glocker, Langleben, Ruparel, Loughhead, Gur, et al., 2009; Hrdy, 1976). Researchers have premised that baby schema features are shared across various species (Borgi et al., 2014; Lorenz, 1943). While baby schema is supposed to exist in various species, many species of primate also display 'infantile coloration', or unique skin and/or coat coloration, during infancy (Booth, 1990; Hrdy, 1976; Ross & Regan, 2000; Treves, 1997). For example, in some colobine species, infants have a bright fur coat while their mothers have a dark coat (Alley, 1980). One plausible functional role of these colorations is to trigger care-taking behaviors in adults. Studies have shown that affiliative behaviors are most often observed toward infants displaying infantile coloration, and decrease as infants age and lose their infantile coloration (Hrdy, 1976). Taken together, both facial shape and color properties can provide critical information related to age, at least in some primate species.

These infantile features are assumed to affect recognition in non-human primates, but it remains unclear whether non-human primates are sensitive to these features for extracting age information. A few studies have reported non-human primates' visual preference for infants. For example, an empirical study with eye-tracking demonstrated that adult chimpanzees (*Pan troglodytes verus*) prefer to look at infant faces when presented with the pictures of conspecific mothers and infants (Chapter 2). However, this preference disappeared when the chimpanzees were presented with grey-scaled images of faces, controlling for face brightness. This suggests that unique infant face color plays an important role in chimpanzees. Visual preferences for infants were also found in Japanese macaques

(*Macaca fuscata*) and Campbell's monkeys (*Cercopithecus campbelli*) (Sato et al., 2012). Furthermore, preference for natal color has been observed in rhesus macaques (*Macaca mulatta*) in one study (Higley et al., 1987), but not in the other (Gerald et al., 2006). Higley et al., (1987) investigated macaques' approach behavior to conspecific infants whose face and/or fur was dyed and reported their attraction to neonatal-like facial skin coloration but not others. On the other hand, Gerald et al., (2006) also tested the role of neonatal color in the same species by presenting digitally color-manipulated face images but found no significant effect of color on rhesus macaques' behavior. Therefore, the evidence on visual preference for natal color is still controversial and has been tested only in limited species.

Although the literature indicates that non-human primates somehow discriminate the age of conspecifics from their appearance, there is little direct evidence that primates are able to explicitly recognize age from faces. It is only recently that humans' ability to distinguish infants from adults by their faces was reported in non-human primates: Kawaguchi, Kuroshima, et al., (2019) trained capuchin monkeys to discriminate between grey-scaled facial images of adults and infants using a symbolic matching-to-sample task and showed that capuchin monkeys can successfully discern adult and infant of human and conspecific faces. Given that the facial images were greyscale, the capuchin monkeys must have extracted facial information besides coloration to discern the age categories of faces.

This begs the question: what kind of facial features are critical to non-human primates' ability to recognize the age of another face? Recent advances in image-processing technology enable researchers to identify which features are important for recognizing various facial attributes (Burt & Perrett, 1995). Humans perceive various facial attributes through a combination of facial shape and color properties (G. Rhodes et al., 2011). Studies on human face perception have investigated how facial shape (e.g., configuration or size of facial parts) and surface (e.g., color or texture) features contribute to age perception. It is shown that facial skin surfaces is a more important cue than facial shape in human age perception: Burt & Perrett (1995) manipulated both facial shape and color separately and found color

had a greater effect than shape on age perception, and Lai et al., (2013) investigated the relative contribution of facial shape and color on age perception and found that texture made greater contribution than shape to age perception.

Although comparative cognitive studies have also studied the role of facial shape (Paukner et al., 2017) and color cues (Waitt & Little, 2006) in the perceptions of facial attributes, the morphing techniques used to manipulate faces' morphology and surface have seldom been applied to non-human primates, with few exceptions. For example, Koba et al., (2009) investigated the role of facial shape on sex discrimination in Japanese macaques. In the study, two Japanese macaques were trained to discriminate between male and female faces. Then, morphed facial stimuli (e.g., a male face with female morphology) were tested and the authors found that the macaques used both morphological and non-morphological cues to discern the sex of the faces. However, they did not address which set of cues was more important for sex discrimination. Therefore, to the best of my knowledge, no study has yet investigated the relative contribution of facial shape and color to facial attributions, especially age perception in non-human primates.

In light of the above, the present study aims to test which aspects of facial features (i.e. facial shape and color) act as cues to age perception via a symbolic matching-to-sample task. Based on previous research which shows that chimpanzees pay attention to infantile facial coloration (Chapter 2), I predicted that the chimpanzees would use facial color as a cue to discern the age category of a face, but did not know whether they would use face shape in the same way. I first trained chimpanzees to discriminate between average adult and infant faces and then tested how they responded to morphed faces with different levels of facial shape and color ranging from adult to infant faces. By using morphed faces, I was able to have systematic control over facial shape and color information and eliminate irrelevant information which occurs and varies randomly across individual facial photographs (e.g., lighting condition). Besides Koba et al., (2009), some other studies have used synthesized face stimuli

such as a morphed or “enhanced” face to study facial recognition in non-human primates (Myowa-Yamakoshi et al., 2005; Parr et al., 2012; Taubert et al., 2017). By testing chimpanzees’ responses to morphed stimuli, this study attempted to determine how important each facial feature is for chimpanzees’ ability to recognize age information in other faces.

4.2 Methods

4.2.3 Participants

Five adult female and one male chimpanzees (aged 18-42 years) participated in the experiment (see Table 4.1). They lived in Kyoto University Primate Research Institute as a social group of 11 individuals. Two of them have given birth before. All the participants were already familiar with cognitive tasks involving touch panels, including matching-to-sample tasks with face stimuli (Dahl & Adachi, 2013; D. A. Wilson & Tomonaga, 2018). One chimpanzee, Ai, used to be trained to use lexigrams for ape-language project (called “Ai Project”) (Matsuzawa, 1989, 1990). She was able to label 67 words representing objects (Asano et al., 1982), color (Asano et al., 1982; Matsuzawa, 1985a), number (Matsuzawa, 1985b), individual (Matsuzawa, 1990) and personal pronouns (Itakura, 1992b). Of the six chimpanzees, three dropped out of the study because they could not pass the criteria set during the very beginning of the training (see Table 4.1 and Appendix for more details). Data from the three remaining chimpanzees is analyzed below. The chimpanzees were housed in an enriched environment which featured both an indoor enclosure and an outdoor compound and vegetation (Matsuzawa, 2006), had free access to water, and received food (fresh fruits, vegetables, sweet potatoes, and nutritionally balanced biscuits) several times each day. All research procedures followed institutional guidelines (Primate Research Institute 2010 version of ‘The Guidelines for the Care and Use of Laboratory Primates’) and the experimental protocol was approved by Animal Welfare and Animal Care Committee of the Primate Research Institute (2019-064) and the Animal Research Committee of Kyoto University.

4.2.4 Apparatus

The experiment was conducted in an experimental booth (1.8m × 2.15m × 1.75m). Each chimpanzee voluntarily came to the experimental booth through a corridor connected to the living areas. A 17-inch touch-sensitive LCD monitor (IO Data LCD-AD172F2-T, 1280 × 1024 pixels) and universal feeder (Biomedica, BFU310-P100) were installed in the booth. I controlled stimulus presentation, response detection, and food delivery by a customized program written in Microsoft Visual Basic 2010 Express working on a personal computer (CPU: Core [TM] i3-4130 3.40 GHz; Intel, Santa Clara, CA).

4.2.5 Stimuli

First, adult and infant chimpanzee faces were averaged across eight individuals (half male, half female). All the pictures were taken by the author or provided by the colleagues. Photographed infants were 2-10 months old and adults were 13-22 years old at the time the pictures were taken. All facial images were scaled and realigned based on eye size and position. To delineate the features of each face, 118 landmarks were placed for each facial image (see Appendix Figure A4.1) with Psychomorph software (Tiddeman et al., 2001), which has been widely used to morph chimpanzee, capuchin monkey, rhesus macaque, and human faces (Damon et al., 2016; Parr et al., 2012; Paukner et al., 2017; Taubert et al., 2017). To average adult and infant face images, I superimposed the adult facial images on one another and the infant facial images on one another. I then morphed the shape and color of these averaged faces. The shape and color of each morphed face independently varied between 0 and 1 (where 0 represents adult features and 1 represents infant features), resulting in 19 morphed faces as illustrated in Figure 4.1. Specifically, these 19 faces consisted of: a) faces with varying facial colors between adult and infant faces with infant facial shapes, b) faces with varying facial colors between adult and infant faces with adult facial shapes, c) faces with varying facial shapes between adult and infant faces with adult facial colors, d) faces with varying facial shapes between adult and infant faces with infant facial

colors, and e) faces with co-varying facial shapes and colors.

To generate training stimuli, I randomly chose three adult faces from a pool of eight adult faces and then created 10 different “three-morphed average adult faces” (see Appendix Figure A4.2). I also created 10 “three-morphed infant average faces” in the same manner. A total of 20 adult and infant average faces were used in the training phase and 19 morphed faces were used in the test phase. Face contours, including ears, did not appear in any of the stimuli since the boundary between face and body was not always obvious in the original pictures.

Two geometric figures (180×180 pixels) were prepared for the comparison stimuli. These geometric figures contained some elements which have been used in “Ai Project” for one of the participant chimpanzees, but the combinations of the elements were unfamiliar to her. One geometric figure was assigned to “adult,” and the other to “infant” and this assignment is consistent among the participants.

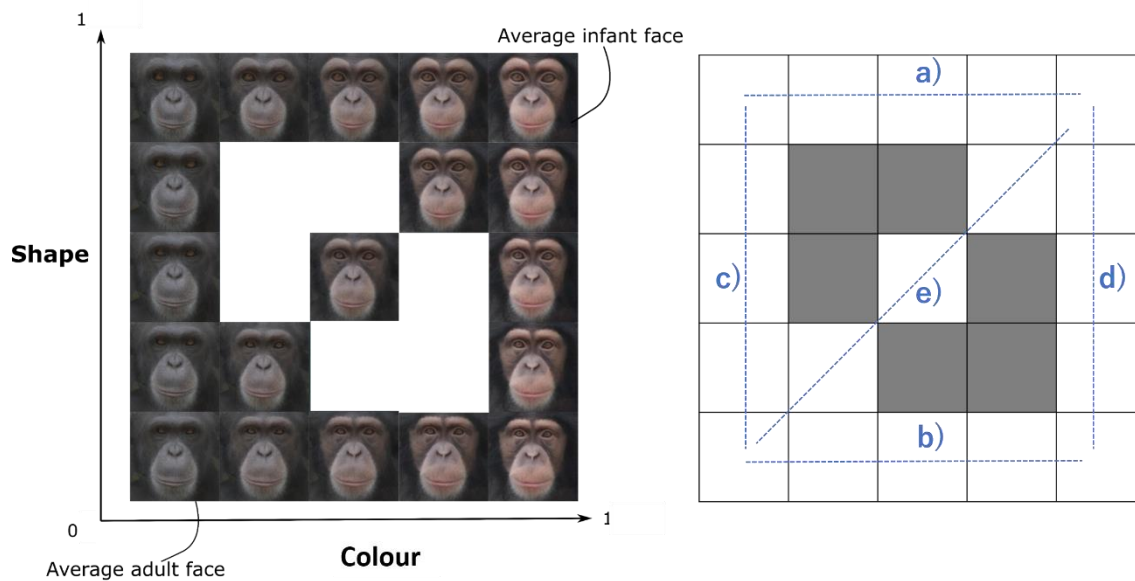


Figure 4.1. The morphed face stimuli used in test phase: a) faces with varying facial colors between adult and infant faces with infant facial shapes, b) faces with varying facial colors between adult and infant faces with adult facial shapes, c) faces with varying facial shapes between adult and infant faces with adult facial colors, d) faces with varying facial shapes between adult and infant faces with infant facial colors, and e) faces with co-varying facial shapes and colors. The facial images were generated with Psychomorph software (version 6; <https://users.aber.ac.uk/bpt/jpsychomorph/>).

4.2.6 Procedure

The chimpanzees were trained to discriminate between adult and infant faces in a zero-delay symbolic matching-to-sample task. In the task, a sample stimulus appeared in the center of the monitor when a chimpanzee touched the self-start key on the bottom of the monitor. Immediately after the chimpanzee touched the sample stimulus, it disappeared and two geometric figures appeared as comparison stimuli – one at each top corner of the monitor (Figure 4.2). The left-right position of the comparison was randomized within each session. When chimpanzees touched the geometric figure which corresponded with the presented image, they received a piece of apple and a chime sound played. When they chose the wrong geometric figure, a buzzer sound was played, no food reward was presented,

and the same trial was repeated as a correction trial. When they made a correct response or made three mistakes, the next trial started. This procedure was almost identical to that of Kawaguchi, Kuroshima, et al., (2019).



Figure 4.2. The procedure of experiment (symbolic matching to sample).

Training Phase

The first training session consisted of 54 trials. Training began by presenting chimpanzees with a pair of three-morphed average adult and infant faces. Adult and infant faces were presented with the same frequency in each session. If a chimpanzee achieved more than 85% accuracy in two consecutive sessions, I considered that they met the training criterion. Then, as a probe test, three new pairs (i.e. six stimuli) were presented for the subsequent two sessions to test the robustness of their ability to discern age from faces. A single probe test session consisted of 18 probe trials and 36 baseline trials. In the probe trials, each new stimulus was presented in three trials as a probe test within a session. In the baseline trials, the learned stimuli were presented. Rewards were delivered regardless of the chimpanzees' choices in the probe trials in order to avoid specific learning for test stimuli, but only correct choices were rewarded in baseline trials. After completing two probe sessions, the chimpanzees were trained with these three pairs besides the learned pairs. The training session consisted of 30 trials with new stimuli and 28 trials with learned stimuli. The combinations of the stimuli pairs were fixed but the order of their introduction was counterbalanced across individuals (Table A4.1). I repeated the training sessions and probe test sessions four times so that the chimpanzees learned 10 stimuli pairs.

Test Phase

When participants' performance met the training criterion for the session including all 10 pairs, test sessions were carried out. A single test session consisted of 19 test trials and 40 baseline trials. Each test stimulus was presented once as the all-reinforced probe test trial in a test session. In baseline trials, training stimuli (i.e. 10 pairs of three-morphed faces) were presented in random order. Test sessions were conducted 16 times in blocks of four sessions. I confirmed the baseline performance before each test block.

4.2.7 Statistical Analysis

Statistical image quantification of adult and infant faces

To ascertain whether there are reliable visual cues to facial differences between adult and infant faces, I performed facial shape and color analysis for the 20 faces (10 adult and 10 infant faces) used as the training stimuli. For the facial shape analysis, all the facial landmarks placed on the 20 faces were superimposed by a generalized Procrustes analysis via tpsRelw software (version 1.65). This analysis was done to standardize face size and optimize face rotation and translation to minimize the distances between corresponding landmarks. Next, I carried out a relative warp analysis (i.e., principal component analysis (PCA) for parameter $\alpha = 0$ via tpsRelw (version 1.65) to reduce dimensionality. The first five components were selected because these components accounted for more than 95% of facial shape variation. To further identify any statistically significant differences between adult and infant facial shapes, I performed Bonferroni corrected t-tests for each of the five shape principal component (PC) scores between the adult and infant faces.

For the facial color analysis, all the facial images were unwarped to the average face configuration across the 20 faces. Next, the RGB color intensity of the facial images was converted into a CIELAB color space. Then, a PCA to the LAB intensity of the facial images was carried out in

MATLAB (version 2019a), and the first seven components were selected because these components accounted for more than 95% of facial color variation. To identify any statistically significant differences between adult and infant facial coloration, I performed Bonferroni corrected t-tests for each of the seven color PC scores between the adult and infant faces.

Behavioral data analysis

The number of correct responses in the probe test during the training session was analyzed via a two-tailed binomial test with 50% as a chance level for each time introducing new stimuli. The number of trials which were judged as ‘infant’ faces for each of the 19-test stimuli was analyzed with a generalized linear mixed model (GLMM) in order to test whether the shape and color of each stimuli affected the chimpanzees’ responses to them. All statistical analyses were conducted on R 3.5.1 (R Core Team, 2018) with the “lme4” package (Bates et al., 2015). For the GLMM analysis, I included the age judgment (infant versus adult, coded as 1 or 0) as a response variable, and the shape and the color score of stimuli as explanatory variables. The shape and color scores were centered by subtracting mean scores, thereby ranging from -0.5 (average adult) to 0.5 (average infant). I also set participant, interaction between participant and shape, and interaction between participant and color as random effects. I used a binomial distribution with a logit link function. I started from the simple model with main effects of shape and color as an explanatory variable, and I tested whether the inclusion of the interaction effect between shape and color improved the goodness of fit of the model by a likelihood ratio test. The likelihood ratio test showed that adding the interaction effect did not significantly improve the goodness of fit ($\chi^2 = 3.2, p = .07$). Therefore, I selected the simple model without interaction effect as the best-fitted model.

4.3 Results

4.3.1 Statistical image quantification of adult and infant faces

To identify the facial features that differed between adult and infant faces, I performed multiple t-tests for facial shape and color components extracted from the PCA. For the facial shape, the five components were individually tested by a t-test with a Bonferroni correction ($0.05/5 =$ a corrected α level of 0.01). The results revealed that infant faces (average = 0.050) had significantly larger PC1 scores than adult faces (average = -0.050) ($p < .001$), while there were no significant differences for any other components (all, $ps > .10$). Facial shape variations along PC1 are visualized in Figure 4.3 (see Figure A4.3 for all five components). Likewise, for the facial color, the seven components were individually tested by a t-test with a Bonferroni correction ($0.05/7 =$ a corrected α level of 0.0071). The results revealed that infant faces (average = -0.22) had significantly smaller PC1 scores than adult faces (average = 0.22) ($p < .001$), while there were no significant differences for any other components (all, $ps > .10$). Facial color variations along PC1 are visualized in Figure 4.4 (see Figure A 4.4 for all seven components).

PC 1 (Contribution 76.34%)

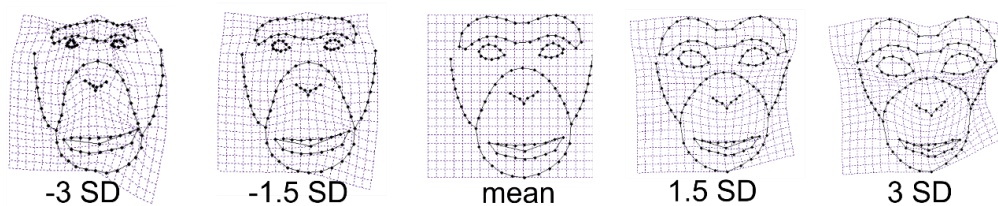


Figure 4.3. Facial shape variations along the axis of the first principal component: The theoretical values of -3, -1.5 SD, average, +1.5, and +3 SD. The facial images were generated with TpsRelw software (version 1.70; <https://tpsrelw.software.informer.com/>).

PC 1 (Contribution 61.58%)



Figure 4.4. Facial color variations along the axis of the first principal component:

The theoretical values of -3, -1.5 SD, average, +1.5, and +3 SD. The facial images were generated with MATLAB

(version 2018a; <https://uk.mathworks.com/products/matlab.html>).

4.3.2 Behavioral task results

Training phase

Three chimpanzees (Ai, Chloe, Pal) completed the all of the sessions. I first investigated the number of sessions each chimpanzee required to learn facial discrimination for each time new stimuli were introduced. Each chimpanzee required 20-49 sessions to learn the first stimuli pair, but required fewer (two to four) sessions as the last new stimuli were introduced (Figure A4.5). Their response accuracy for the unfamiliar face stimuli in the probe test trials during the training phase was significantly above the chance level ($p < .05$) each time introducing from the beginning in all three chimpanzees (Figure A4.5). Visual inspection of the results revealed that Ai, a chimpanzee who had previous language training required slightly fewer sessions to reach the learning criteria than other two chimpanzees, but her performance for unfamiliar stimuli was not considerably different from others.

Test phase

Figure 4.5 illustrates the number of responses judged as ‘infant’ for each test stimulus in the test phase. I analyzed the number of ‘infant’ responses with GLMM. The best-fitted model included the main effects of shape and color score, but not the interaction effect between shape and color scores. The

GLMM analysis showed the significant main effect of shape ($\beta = 0.66, z = 2.79, p = .005, 95\%$ confidence interval (CI) [0.19, 1.12]), and significant effect of color ($\beta = 5.08, z = 10.60, p < .001, 95\%$ CI [4.14, 6.02]; Table 4.2). The odds ratio (OR) of the main effect of shape was 1.92 (95% CI [-1.21-3.07]) while that of color was 160.93 (60.31-471.60), suggesting that the OR of color was 83 times bigger than that of shape in the chimpanzees' responses. Again, visual inspection of the results found no considerable difference between Ai and the other two chimpanzees.

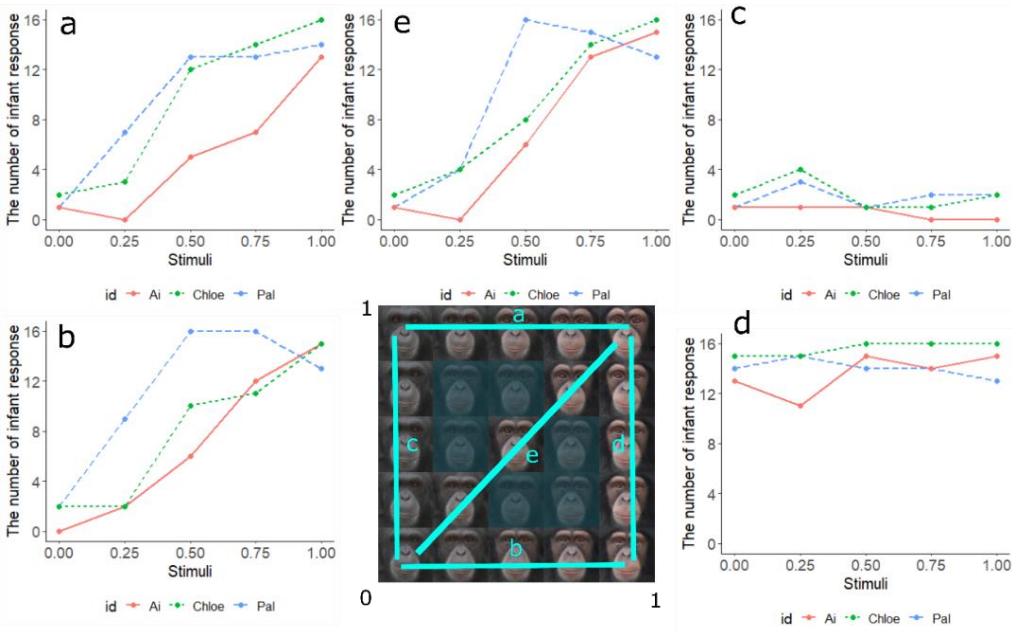


Figure 4.5. The number of infant responses for each stimulus in 16 trials. A) Color effect on infant shape, b) Color effect on adult shape, c) Shape effect on adult color, d) Shape effect on infant color, e) Color and shape effect

4.4 Discussions

The present study aimed to investigate the relative contributions of facial shape and color to chimpanzees' ability to discern age category from facial images by using a series of morphed face stimuli that differ in facial shape and color. The results indicate that both facial shape and color are critical cues to chimpanzees' age judgments, but facial color has a greater impact on these judgements than shape.

These results are consistent with the results of the previous study (Chapter 2), which found that chimpanzees allocate more attention to unique infant face coloration. The results further demonstrated that facial color contributes more than facial shape on discriminating adult and infant faces. It is of note that at least three chimpanzees learned to discriminate adult and infant faces and were able to generalize the categorization to unfamiliar stimuli in the training phase. These results indicate that chimpanzees can visually dissociate adults and infants from facial appearance.

Statistical quantification of the facial images revealed that there are critical differences in the shape and color of adult and infant chimpanzees' faces. Image analysis of facial shapes revealed the first principal component (PC 1) significantly differed between adult and infant faces. As illustrated in Figure 4.3, the positive PC1 score (i.e. more infantile faces) was characterized by a baby schematic configuration, such as bigger eyes located in a relatively lower position on the face. In addition, infant chimpanzee faces have a curved supraorbital torus but adult chimpanzee faces do not. Meanwhile, the image analysis of facial color also revealed that PC1 scores significantly differed between adult and infant faces. As illustrated in Figure 4.4, the negative PC1 score was characterized by an infantile coloration, such as brighter skin color.

As far as I know, this study is the first to quantify developmental changes in facial surface in chimpanzees. Although a number of studies have focused on the cognitive processing of infantile shape features (i.e. baby schema) in human faces (Alley, 1981, 1983a, 1983b; Borgi et al., 2014; Burt & Perrett, 1995; Glocker, Langleben, Ruparel, Loughead, Gur, et al., 2009; Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009; Hildebrandt & Fitzgerald, 1979; Hrdy, 1976; Little, 2012) and non-human animal faces (Borgi et al., 2014; Borgi & Cirulli, 2013; Little, 2012), each of these studies have restricted themselves to human perception of facial features. Moreover, roles of infantile coloration, or species-specific infantile face features have received less attention and only been tested in rhesus macaques (Gerald et al., 2006; Higley et al., 1987). My data showed the importance of taking species-

specific features into account when attempting to determine how non-human primates discern age from faces. Taken together with this study's findings, it can be concluded that infant chimpanzees' faces have species-general infantile features characterized by the baby schema, and that they also have species-specific infantile features such as a unique supraorbital torus or face coloration.

The results of the behavioral task showed that chimpanzees are able to differentiate between adult and infant faces. This finding is consistent with previous studies of capuchin monkeys (Kawaguchi, Kuroshima, et al., 2019), where monkeys learned to discriminate adult and infant faces of conspecifics. This study indicated that chimpanzees pay attention to infantile face coloration and use it as a cue to differentiate between age categories of faces. Of particular interest is that not only color cues, but also shape cues existed in chimpanzee faces for age categorization but color had greater effect than shape in this regard. This might be because chimpanzees are attuned to species-specific facial coloration which has been uniquely acquired (or retained) through their evolution. I cannot conclude why the effect of color cue was more dominant than that of shape from this experiment. Facial color can be more prominent and reliable cues than shape in their living environment when chimpanzees need to extract age information from other individuals with some distance. At the same time, it is also known that chimpanzees have some facial skin color variations even among adults and that they likely use these to recognize and distinguish between individuals (Bradley & Mundy, 2008). Chimpanzees may be particularly sensitive to an individual's facial coloration in general because it tells them a lot about the individual in question.

Then, what does facial coloration tell chimpanzees about the age of a given face? Infantile facial coloration lasts into adolescence to some extent and takes longer to fade into adult coloring in chimpanzees than it does in many other primate species which also have infantile coloration. Given the nature, they may be able to get not only rough information from faces on whether the individual is infant or adult, but more precise information such as specific age class (e.g., late infancy) s/he belongs to.

Another study revealed that the face coloration of Borneo orangutans (*Pongo pygmaeus*) change as they age until around 10 years old (Kuze et al., 2005). This indicates that face coloration may turn out to be a reliable indicator of developmental stage in non-human primates. Kuze et al. (2005) pointed out that infants and juveniles may enjoy tolerance from other individuals in social context thanks to this age signal. This may be also true for chimpanzees; displaying their age class by facial color may benefit not only chimpanzee infants, but also juveniles in certain social contexts such as mating or group transfer, although it is outside the scope of this study. There have been many debates on the general function of infantile coloration such as inducing alloparenting, preventing aggression, hiding paternity and so on (Alley, 1980; Booth, 1990; Hrdy, 1976; Ross & Regan, 2000; Treves, 1997). The display of their developmental stages through facial color may help chimpanzees to induce contextually appropriate behavior from other individuals. Nevertheless, the clear and precise function of infantile coloration remains an open question.

This study has a few limitations. First, I acknowledge that the sample size was quite small because of the difficulty of the task employed in the study (i.e. zero-delayed symbolic matching-to-sample). The sample size was as small as that in similar demanding tasks in previous non-human primate studies (e.g., two Japanese macaques (Koba et al., 2009), three chimpanzees (Parr, 2004)). Given that the results among the three individuals were consistent, however, it is likely that the results reflect robust tendencies. Second, I could not conclude whether chimpanzees performed age categorization based on something like the age category concept or merely by combining low-level visual properties of the stimuli. It could be possible to address this point by testing generalizations to other types of stimuli (e.g., whole body images or vocalizations of adults and infants). Even if their discrimination was not based on some concept of age, this would not alter the fact that they successfully differentiated between adult and infant faces and likely use the same features in their real life because such features are salient to them.

The present study showed that it is feasible to study face recognition in non-human primates in a similar manner to humans by using well-controlled face stimuli, namely morphed faces to dissociate the effect of facial features such as shape and color. Dissociating the effects of facial shape and color on facial attributes has been a predominant method in face studies since it was first proposed by D. A. Rowland & Perrett, (1995), but it has only rarely been adopted in studies of non-human primates. Such an approach will enable us to investigate how each of facial features affects non-human primates' facial recognition with various dimensions. Although the current study suggests that facial coloration is a critical element of age categorization in chimpanzees, whether it also plays an important role in other general attributes is unclear. In humans, how much shape and color information contribute to face perception varies across facial attributes to be judged. For example, past studies have shown that facial shape plays a more important role than color in determining notions of 'female dominance' and 'identity', but the opposite is true for 'male attractiveness' and 'perceived age' (Lai et al., 2013; Torrance et al., 2014). Future studies should address whether chimpanzees and other non-human primates rely more on facial shape information rather than color when judging other aspects of faces such as sex, attractiveness, or identity. Of course, this approach is not limited to chimpanzees, but applicable for other non-human primates. For example, it is known that both facial redness and symmetry contribute attractiveness in rhesus macaques (Waite et al., 2003; Waite & Little, 2006), but it has been unclear which is more important for them. Using a morphing technique as I did in this study will deepen our knowledge on face processing in non-human primates.

4.5 Tables

Table 4.1. Participant information.

Individual name (GAIN ID ^a)	Sex	Age	Birth experience	Training
Ai (0434)	Female	42	Parous	passed
Chloe (0441)	Female	38	Parous	passed
Pal (0611)	Female	19	Nulliparous	passed
Cleo (0690)	Female	19	Nulliparous	dropout
Pendesa (0095)	Female	42	Nulliparous	dropout
Ayumu (0608)	Male	19	-	dropout

^a Individual information based on the database of GAIN (Great Ape Information Network).

Table 4.2. The results of the GLMM analysis.

<i>Factor</i>	<i>Estimate</i>	<i>SE</i>	<i>Z</i>	<i>p</i>	<i>95 % Confidence Interval</i>
Intercept	0.11	0.40	0.28	0.78	[-0.67, 0.89]
Color	5.08	0.48	10.60	<.001	[4.14, 6.02]
Shape	0.66	0.24	2.19	0.005	[0.19, 1.12]

4.6 Appendix

Supplementary Note

During the training, three chimpanzees (Cleo, Pendesa and Ayumu) dropped out because their performance did not sufficiently improve after 15 consecutive 'block-sessions' when they were trained to discriminate the first stimulus pair. In a block-session, one session was divided into two to six blocks and the same sample stimulus was presented within one block. I started with a two-block session in which one stimulus was presented in the first half trials and the other stimulus was presented in second half trials in one session. If their performance achieved the criterion (more than 85 % in two consecutive sessions), I conducted the next block session where one session was divided into more blocks (i.e. a four-block session or six-block session) which means the same stimulus presented fewer consecutive trials.

Supplementary Figure

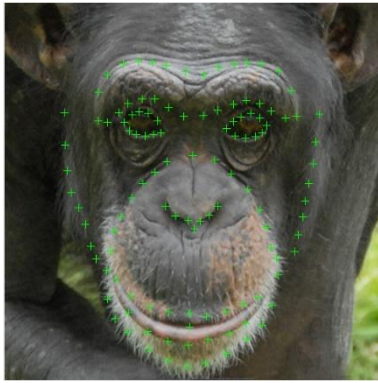


Figure A4.1. An example of facial landmarks. The landmarks were placed with Psychomorph software (version 6; <https://users.aber.ac.uk/bpt/jpsychomorph/>).

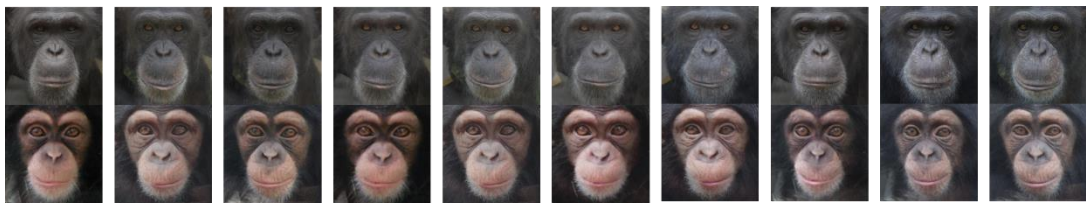
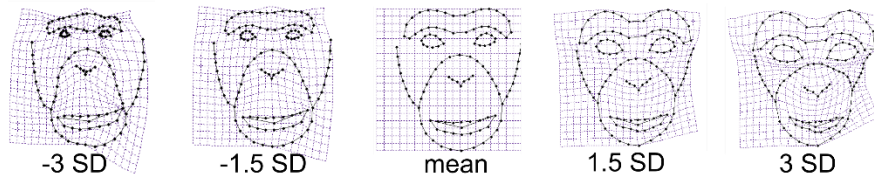
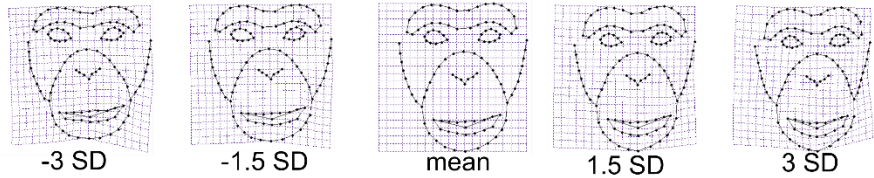


Figure A4.2. The 10 pairs of three-morphed average faces used for training and image analysis. The facial images were generated with Psychomorph software (version 6; <https://users.aber.ac.uk/bpt/jpsychomorph/>).

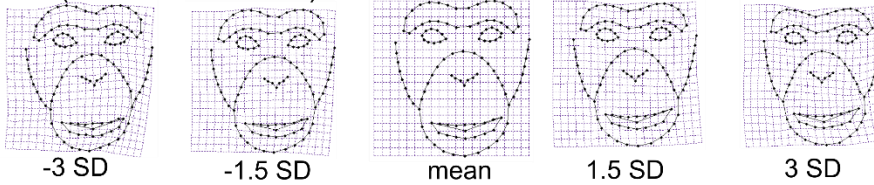
PC 1 (Contribution 76.34%)



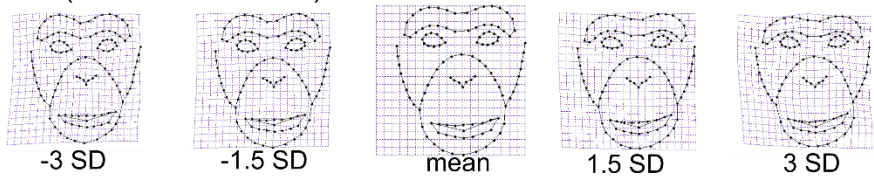
PC 2 (Contribution 6.99%)



PC 3 (Contribution 5.70%)



PC 4 (Contribution 3.89%)



PC 5 (Contribution 2.70%)

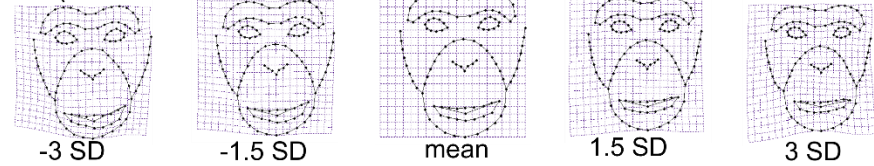


Figure A4.3. Facial shape variations along the axis of the principal components.

These first five components accounted for more than 95% of facial shape variation in total: The theoretical values of -3, -1.5 SD, average, +1.5, +3 SD. The facial images were generated with TpsRelw software (version 1.70; <https://tpsrelw.software.informer.com/>).

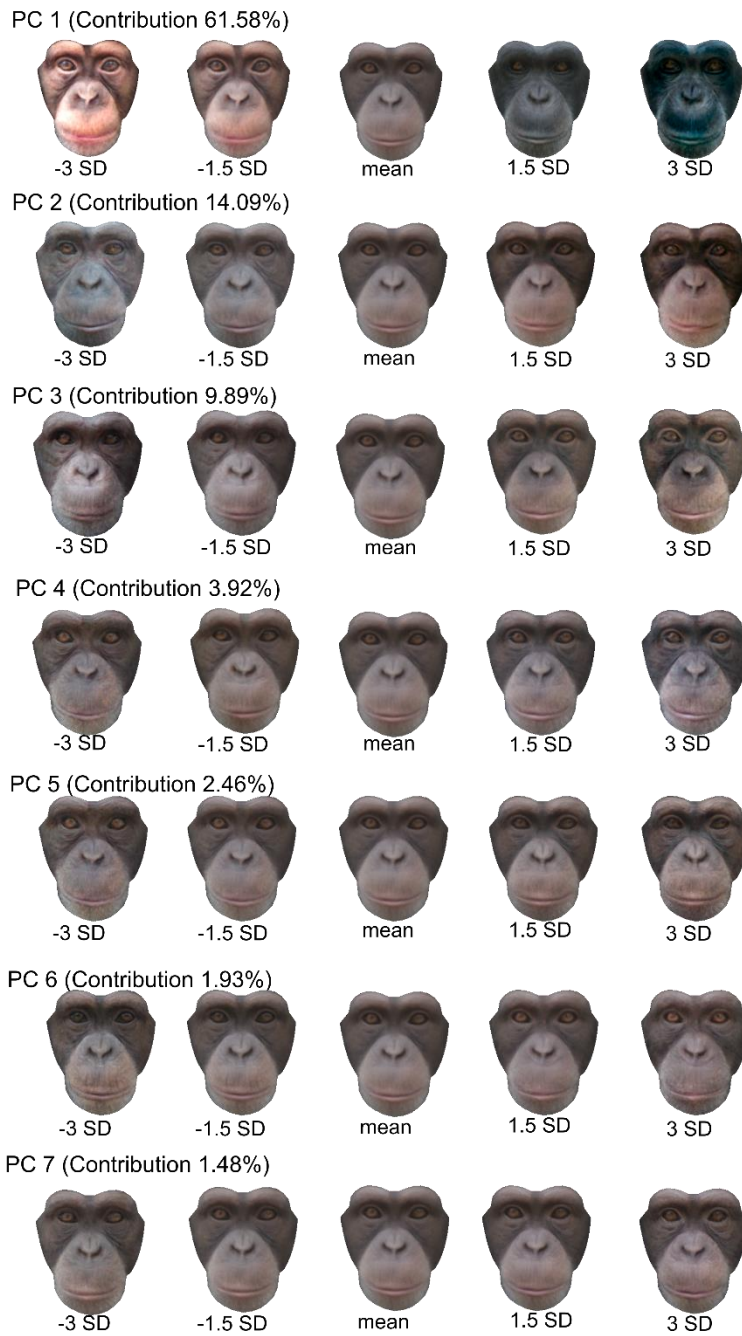


Figure A4.4. Facial color variations along the axis of the principal components.

These first seven components accounted for more than 95% of facial shape variation in total: The theoretical values of -3, -1.5 SD, average, +1.5, +3 SD. The facial images were generated with MATLAB (version 2018a; <https://uk.mathworks.com/products/matlab.html>).

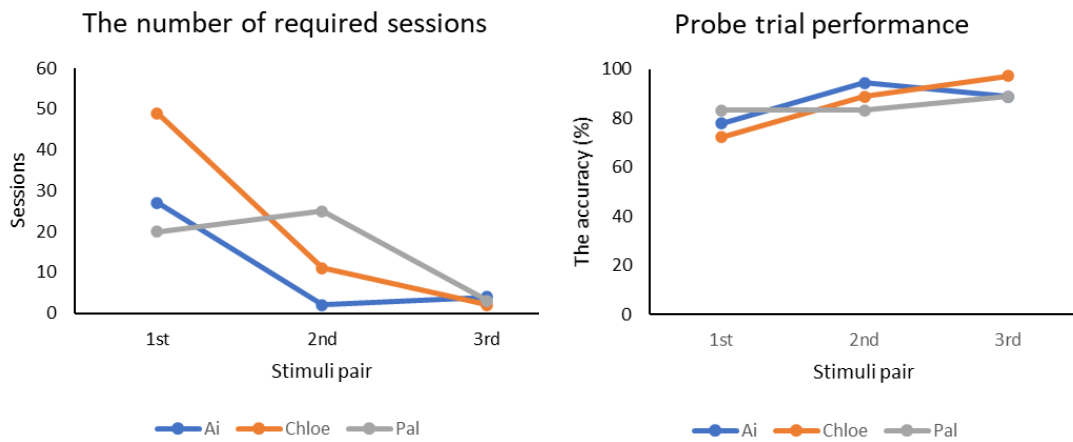


Figure A4.5. The number of required sessions for reaching the learning criteria (left) and the performance of probe trials during the training (Right).

Table A4.1. The order of the stimuli pairs used in the training phase

	Ai	Ayumu	Chloe	Cleo	Pal	Pen
Step 1	pair 1	pair 1	pair 7	pair 7	pair 4	pair 4
Step 2	pair 2, 3, 4	-	pair 2, 4, 10	-	pair 1, 2, 10	-
Step 3	pair 5, 6, 7	-	pair 5, 6, 8	-	pair 3, 5, 7	-
Step 4	pair 8, 9, 10	-	pair 1, 3, 9	-	pair 6, 8, 9	-

Chapter 5: No Evidence on Spatial Representation about Age, but “Own-Age Bias” like Face Processing in Chimpanzees

5.1 Introduction

Faces convey a lot of information to humans, which includes age, identity, gender, emotional states, and so on (Bruce & Young, 2012; G. Rhodes et al., 2011). Non-human primates can also extract various information from faces (Adachi & Tomonaga, 2017; Leopold & Rhodes, 2010; Parr, 2011). This includes identity (Itakura, 1992a; Parr et al., 2000), species (D. A. Wilson & Tomonaga, 2018), sex (de Waal & Pokorny, 2008; Koba et al., 2009), social rank (Dahl & Adachi, 2013), emotional states (Kanazawa, 1996; Parr, 2003), attentional states (Tomonaga & Imura, 2010), attractiveness (Waite et al., 2003), and so on. However, facial age perception has not been studied in non-human primates until quite recently even though it is one of the well-studied topics in human face recognitions (e.g., Burt and Perrett 1995; for review Rhodes 2007). Recognizing conspecific’s approximate age, such as age category is important for social primates as it enables them to behave appropriately around other individuals by changing their behavior based on it (Berry & McArthur, 1986). An infant individual should be differently treated from an adult individual by conspecifics for example in that s/he is vulnerable and cannot survive without care from adults. Non-human primates may use various cues such as body size, body movement, vocalization, odors, but facial cues can also provide reliable information on age.

Some studies investigated how non-human primates respond to face stimuli of adult and infant individuals. Koda et al. (2013) examined whether Japanese macaques (*Macaca fuscata*) exhibit an attentional bias for infant faces, which has been reported in humans (Lucion et al., 2017), but they obtained no evidence to support this. My previous studies found that non-human primates have the

ability to differentiate between faces of different age categories (i.e., adult or infant) (Kawaguchi, Kuroshima, et al., 2019, Chapter 4). In these studies, chimpanzees (*Pan troglodytes*) (Chapter 4) and capuchin monkeys (*Sapajus apella*) (Kawaguchi et al., 2019) were trained to discriminate between the adult and infant faces of conspecifics or humans by using a symbolic matching-to-sample task. Both the chimpanzees and capuchin monkeys easily learned to do this and this ability was generalized to the discrimination of novel stimuli. These studies clearly show that the sensitivity to age-related facial features is shared by non-human primates and they discussed what kind of facial cues they seemingly used for such categorization. However, compared to the accumulation of human literatures, there are still limited understandings of the perception of facial age in non-human primates. Even though previous studies have found that non-human primates are able to visually differentiate adult faces and infant faces, it is still unknown whether non-human primates extract an age category concept from faces. They may have categorized adult and infant faces just by combining low level features without recognizing age. Therefore, I asked this by testing spatial mapping of face age in chimpanzees.

As illustrated by the idiom “from the cradle to the grave,” humans recognize that infants and adults exist linearly in a time sequence. In other words, we understand that an infant will not have been an infant forever and that an elderly person was not elderly when s/he was born. Moreover, when people illustrate human life stages, in most cases, the infant is depicted on the left, the “middle” age is placed on the middle, and the elderly person is presented on the right in a horizontal line. This is because we have a mental timeline and we associate space and time in a certain direction (e.g., earlier is left; later is right) (Fuhrman & Boroditsky, 2010; Santiago et al., 2007; Torralbo et al., 2006; Weger & Pratt, 2008). For example, Fuhrman & Boroditsky (2010) presented pairs of pictures one after another, and the participants were required to answer whether the second picture showed either an “earlier” or “later” event than the first picture by pressing keys. The stimuli were including both representing short (e.g., filling a cup of coffee) and long (e.g., human of different age class) period of time. English speakers

were faster to make earlier judgement when the corresponding key was positioned at the left than the right, while Hebrew speakers showed exactly the opposite pattern. Thus the direction of such a mental timeline is influenced by the writing direction in the culture. Furthermore, a larger congruency effect was observed when the stimuli depicted a long-time interval. Spatial representation of time is observed not only horizontally but also vertically in some cultures (e.g., Boroditsky 2001). Moreover, the correspondence between the abstract domain and spatial domain is observed not only for time but also for other abstract domains including such as number (for a review see Fias & Fischer, 2005), social rank (e.g., Schubert, 2005), auditory pitch (e.g., Rusconi et al., 2006), and so on. Each abstract domain is mapped horizontally, vertically, or both. One example of vertical conceptual metaphorical mapping is social status. It is known that “high-ranked” individuals are represented in spatially higher positions than “low-ranked” individuals by human adults (Schubert, 2005).

Although the orientation of the abstract domain’s spatial representation is often influenced by culture or experience (e.g., Shaki & Fischer, 2008), the correspondence between the abstract domain and spatial domain is also observed in non-human animals at least to some extent. For example, there is some evidence of the spatial mapping of numbers in chicks (Rugani et al., 2015, 2017), rhesus macaques (Drucker & Brannon, 2014) and chimpanzees (Adachi, 2014). Furthermore, Dahl and Adachi (2013) found that chimpanzees also have the similar spatial mapping of the dominance hierarchy as humans. They conducted a matching-to-sample task in which chimpanzees were required to discriminate between the face identities of familiar group members that were presented in a vertical arrangement. They reported that when the rank of the represented individual and the position in the display were congruent (e.g., a high-ranked individual was positioned higher), the response time was faster than when they were incongruent. These comparative studies suggest that space-based representations have emerged before language evolution although language may have utilized and expanded the existing space-based representations. However, it is unknown whether non-human primates have a particular spatial

representation of age.

One of the aims of this study was to investigate whether chimpanzees spatially represent conspecifics' adult and infant faces. The rationale is that, if chimpanzees refer, from a face, conceptual age category which can be recognized in time sequence, and if they have space-based representation of time like a mental timeline in humans, they would respond faster when the spatial arrangement of face stimuli are congruent with their mental timeline. It should be noted that previous studies have demonstrated that spatial and time judgments interact with each other in rhesus macaques (Mendez et al., 2011; Merritt et al., 2010). However, as far as I know, there is no study investigating a space-based representation of time in non-human primates.

Although testing spatial mapping of face age was the main purpose of this study, I also investigated whether chimpanzees show asymmetric performance between discriminating adult faces and infant faces because it is known that face processing is largely modulated by the amount of the experiences. Enhanced experiences of the certain face category both in early and late lifetime selectively tune perceptual systems for face processing toward that category. For example, older infants (9-month-old) and adults can discriminate among conspecific faces but not monkey faces while younger infants (6-month-old) can discriminate both of them (Pascalis, 2002). Such perceptual tuning based on very early experience in life is called as perceptual narrowing and also observed for other face categories such as own- versus other- race faces in humans ("own-race bias", e.g., Kelly et al. 2007). On the other hand, besides such early perceptual tunings, later exposure or expertise throughout lifetime also modulates face processing. For example, Koreans living among Caucasians from their childhood show better performance for identifying Caucasian faces rather than the Asiatic faces (Sangrigoli & Pallier, 2005). Enhanced face processing by extensive exposure in later life is also known toward faces of the certain age category and called "own-age bias (Wright and Stroud, 2002)". This bias is the phenomenon in which human adults show superior processing for adult faces compared with their processing for

children's faces and vice versa. It is considered that such bias, like other biases in face processing, results from more frequent exposure to individuals from the same category (i.e., a similar age group) than to others in daily social life (M. G. Rhodes & Anastasi, 2012). This is because preschool teachers, for instance, can recognize children's faces as well as adults' faces (Kuefner et al., 2008).

The enhanced face processing by both early and late exposure of the certain face category is reported in non-human primates. Dahl and his colleagues investigated captive chimpanzees' face discrimination ability for both conspecifics and humans (Dahl & Adachi, 2013). They found that young chimpanzees with less exposure to humans show advantage in discriminating chimpanzees than human faces, while adult chimpanzees with lifelong exposure to humans show advantage for human faces than conspecific faces. Yet it remains unknown whether the amount of experience of the certain age category also affects face processing efficiency in non-human primates. Therefore, I compared the performance of adult chimpanzees when they discriminated between adult faces and infant faces in order to explore whether they also exhibit this age-related asymmetric processing efficiency.

In order to investigate those two aspects, namely spatial mapping and the amount of exposure related to age, I used a matching-to-sample task in which chimpanzees were required to match the faces of either adult or infant individuals. I applied and modified the procedure of Dahl and Adachi's previous study, which reported the vertical representation of dominance in chimpanzees (Dahl & Adachi, 2013). In the matching-to-sample task, two comparison images were presented in vertical (Experiment 1) or horizontal (Experiment 2) arrays. I examined whether their performance differed depending on the correspondence between the position and the age category of the stimuli. To examine the spatial correspondence effect, the two comparison images were from different age categories (i.e. one adult and one infant) in one condition and they were from the same age category in the other condition. I also compared their discrimination performance for adult faces and that for infant faces in order to know if they show age-related asymmetric processing efficiency based on the different amount of the

experiences.

5.2 Methods

5.2.1 Participants

Six chimpanzees (*Pan troglodytes verus*) who were living in the Primate Research Institute, Kyoto University, participated in the experiments. All of them were adults (17–41 years old) and one was male (see Table 5.1 for more individual information). They are living as a social group including 11 adult individuals. The chimpanzees live in an enriched environment with an outdoor compound (700 m²) and an indoor enclosure. They also have access to a semi-outdoor residence (Matsuzawa, 2006). They are neither food- nor water-deprived and they live in social groups. They receive food several times each day and they always have access to water.

The participants were called for the experiments daily and their participation was voluntary. During the experiment, they were unrestrained and they could stop the task whenever they wanted to. All of them had abundant experience of matching-to-sample tasks, including in Dahl and Adachi's previous study. All procedures adhered to institutional guidelines (the Primate Research Institute's 2010 version of "The Guidelines for the Care and Use of Laboratory Primates"). The experimental design was approved by the Animal Welfare and Animal Care Committee of the Primate Research Institute (2018-115) and the Animal Research Committee of Kyoto University.

5.2.2 Apparatus

All of the experiments were conducted in experimental booths (1.8 m wide × 2.15 m deep × 1.75 m high). The participants were tested using touch-sensitive 17-inch LCD monitors (LCD-AD172F2-T monitor, 1280 × 1024 pixels) and universal feeders (BUF-310, Biomedica). The stimuli presentation, touch detection, and reward delivery during the experiments were controlled using personal computers (PC-9821 Xn, NEC Corp.). The experimental program was written in Microsoft

Visual Basic 2010 Express (Microsoft Corp.).

5.2.3 Stimuli

I used six adult and six infant chimpanzee face images as the stimuli. Most of the photographic images were either taken by the author or provided by colleagues, while a few were obtained from public sources. The depicted individuals were unfamiliar to the participants and they showed neutral expressions. Half of the adult chimpanzees were males while the sex of some of the infant chimpanzees was unknown. Unfortunately, the exact ages of some of the infants in the images taken from public sources were also unknown. However, I selected pictures of infants who were/appeared to be younger than 2 years old when they were taken. Using Adobe Photoshop Elements 15 (Adobe Inc., San Jose, CA, USA), all of the images were cropped into a square with 250×250 pixels ($6.6 \text{ cm} \times 6.6 \text{ cm}$), their luminance was matched, and they were presented in color.

5.2.4 Procedure

The participants were required to perform an identical zero-delay matching-to-sample task (Figure 5.1). Each trial began when the participant touched the self-start key that appeared at the bottom of the monitor after a 2 sec inter-trial interval. The self-start key appeared twice in different positions at the bottom of the monitor, with the second one always being presented in the center of the bottom of the monitor. When they touched the start keys, a sample image appeared in the center of the monitor for 750 ms. Two comparison images then appeared, one of which was identical to the sample stimulus. The participants were required to choose the same image. When they chose the correct answer, a piece of apple was delivered via the universal feeder as a reward.

In Experiment 1, the two comparison images were presented in a vertical array, while in Experiment 2, they were presented in a horizontal array. In both experiments, the two comparison images were from the same age category (i.e., both were adults/both were infants) in the same condition and they were from a different age category (i.e., one was an adult and the other was an infant) in the different

condition. In each experiment, there were a total of 66 combinations of the comparison images, since there were 12 stimuli in total. For each combination, there were two comparison arrays (top or bottom in Experiment 1/left or right in Experiment 2) and two sample stimuli (either of the comparison images). Hence, the total 264 trials were divided into six sessions. In one session, 20 trials were presented in the same condition and 24 trials were presented in the different condition. The order of the conditions and stimuli was pseudo-randomized.

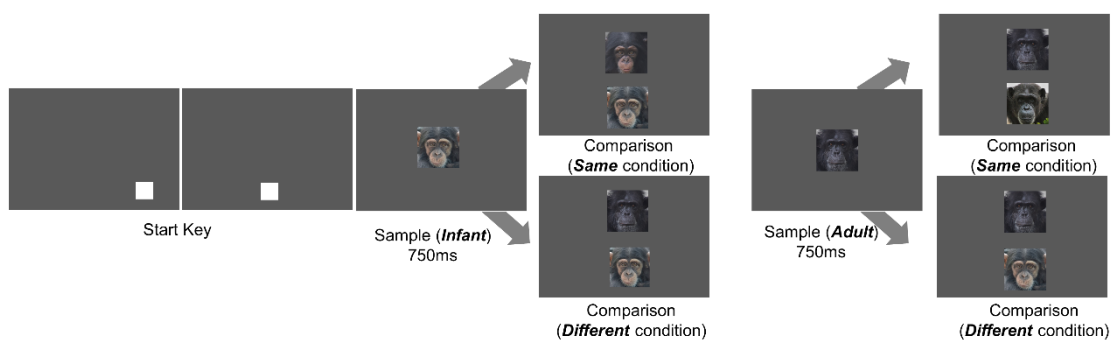


Figure 5.1. An example of one trial in Experiment 1 (vertical array). The self-start key was presented at the bottom. When the participant touched it, a sample stimulus was presented in the center of the monitor for 750 ms. When the sample disappeared, two comparison images were presented and the participant was required to touch the same stimulus. In the same condition, the two comparison images were from the same age category, while in the different condition, they were from different age categories.

5.2.5 Data Analysis

Behavioral Data Analysis

In both experiments, the number of correct responses and the response times to choose the correct answers were analyzed. The number of correct answers was calculated for each condition and I conducted a $2 \times 2 \times 2$ ANOVA of the position (top or bottom/left or right), age of the stimuli (adult or infant), and condition (same or different) as the independent variables. For the response time, only the response times of the correct trials were analyzed. I excluded response times that were longer than the

average value plus three standard deviations (*SDs*) since the chimpanzees were sometimes distracted by unexpected noise from outside or by something else during the experiment and took longer to respond. The response time was analyzed using a $2 \times 2 \times 2$ ANOVA with the same independent variables as the analysis of the performance. All the statistics were conducted by R 3.5.1 (R Core Team, 2018).

Image Analysis

When a different performance of the discrimination between adult and infant faces was found, I could not deny the possibility that this asymmetry may simply be caused by the variation in the physical characteristics of the infant faces just being smaller than that of the adult faces. In order to compare the physical variation in the face stimuli within each age category, I conducted an image similarity analysis of the stimuli and compared it between the age categories. The similarity between each exemplar (adult faces [$n = 6$] and infant faces [$n = 6$]) was evaluated for all combinations within the same age category. I used the structural similarity index ("SSIM," Wang et al., 2004), which is widely used to measure the similarity of two images by comparing local patterns of pixel intensity. The analysis was conducted using Python (Python Software Foundation, Wilmington, DE, USA) and OpenCV (Intel Corp., Santa Clara, CA, USA). All stimuli were converted to grayscale and the SSIM was calculated for all of the possible combinations. The SSIM could range from -1 to +1, and if the two images were identical the score was 1. In order to calculate the physical distance between each of the stimuli, this SSIM score was subtracted from 1. The calculated differential score between every stimulus combination within each age category was compared using the Mann-Whitney U-test.

5.3 Results

5.3.1 Behavioral data

Experiment 1 (Vertical Array)

I analyzed the number of correct answer by a repeated-measures ANOVA and found a

significant main effect of condition ($F_{1,5} = 207.44, p < .001, \eta^2_p = 0.98$), and approached significant main effect of age ($F_{1,5} = 4.97, p = .08, \eta^2_p = 0.50$), and approached significant interactions between condition and age ($F_{1,5} = 4.97, p = .08, \eta^2_p = 0.50$), but the other main effect and the interactions were not significant (all $ps > .10$). The post-hoc analysis (adjusted using Shaffer's procedure) indicated the effect of condition was statistically significant both of when the stimuli were adults ($F_{1,5} = 764.10, p < .001, \eta^2_p = 0.99$) and infants ($F_{1,5} = 477.04, p < .001, \eta^2_p = 0.94$). The effect of age was approached significant when the condition was same ($F_{1,5} = 4.97, p = .08, \eta^2_p = 0.50$), but not significant when the condition was different because the performance was perfect for both of adults and infants in the different condition.

A repeated-measures ANOVA of the response time revealed a significant main effect of position ($F_{1,5} = 7.19, p = .04, \eta^2_p = 0.59$) (Figure 5.2, see also Figure A5.1 for individual data) and condition ($F_{1,5} = 30.07, p = .003, \eta^2_p = 0.86$), and approached significant main effect of age ($F_{1,5} = 6.40, p = .05, \eta^2_p = 0.56$) and the approached significant interaction between condition and age ($F_{1,5} = 4.89, p = .08, \eta^2_p = 0.49$). The other interactions were not significant (all $ps > .10$). The post-hoc analysis indicated that the effect of condition was statistically significant when the stimuli were infants ($F_{1,5} = 67.36, p < .001, \eta^2_p = 0.93$), but that it was not significant when the stimuli were adults ($F_{1,5} = 4.05, p = .10, \eta^2_p = 0.45$). The effect of age was significant in the same condition ($F_{1,5} = 8.11, p = .04, \eta^2_p = 0.62$), but not significant in the different condition ($F_{1,5} = 0.16, p = .71, \eta^2_p = 0.03$).

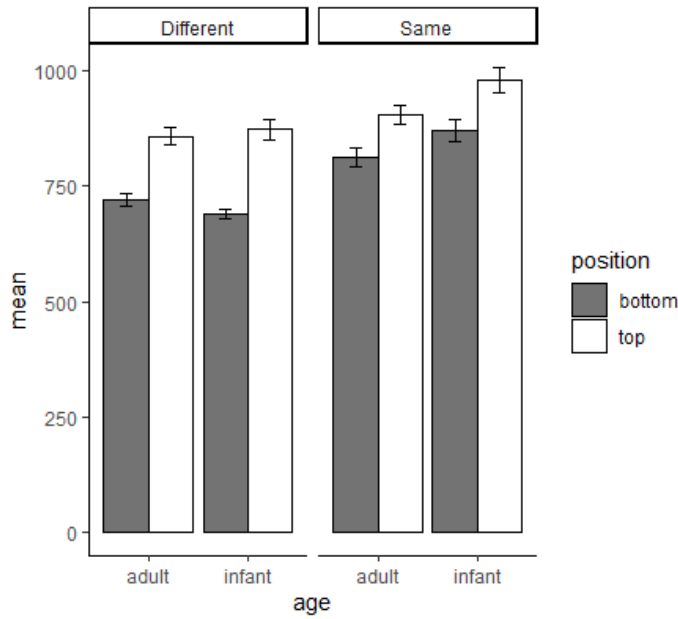


Figure 5.2. The average response time in Experiment 1 (vertical array). The error bars indicate the standard error.

These results indicated the following. First, the response time when the target was presented at the top of the monitor was consistently longer than when it was presented at the bottom (i.e., the significant effect of position). This probably occurred as touching the top part of the monitor was simply physically more demanding, because of the touch panel’s structure. Second, differentiating between faces from the same age category was more difficult than differentiating between faces from different age categories (i.e., the significant effect of condition). This suggests that the faces from the different age categories were perceptually more different to each other than those from within the same age category. Third, the chimpanzees took more time when the target was an infant than when it was an adult, especially when they needed to discriminate between two different infant faces (i.e., the approached significant interaction effect between age and condition). On the other hand, the results did not show a congruency effect between the target’s age and position (i.e., no significant interaction effect between age and position). Hence, there was no evidence of correspondence between vertical space and adult/infant faces.

Experiment 2 (Horizontal Array)

I analyzed the number of correct answer by a repeated-measures ANOVA and found a significant main effect of condition ($F_{1,5} = 188.53, p < .001, \eta^2_p = 0.97$), but the other main effect and the interactions were no significant (all $p_s > .10$). This main effect of condition indicates the performance in the different condition was better than that in the same condition.

A repeated-measures ANOVA of the response time revealed a significant main effect of condition ($F_{1,5} = 27.47, p = .003, \eta^2_p = 0.85$), but not of position ($F_{1,5} = 0.35, p = .58, \eta^2_p = 0.07$) or age ($F_{1,5} = 1.74, p = .24, \eta^2_p = 0.26$) (Figure 5.3, see also Figure A5.1 for individual data). The interaction between condition and age was significant ($F_{1,5} = 12.15, p = .02, \eta^2_p = 0.71$), but the other interactions were not (all $p_s > .10$). The post-hoc analysis indicated that the effect of condition was significant for the adult stimuli ($F_{1,5} = 11.43, p = .02, \eta^2_p = 0.70$) and for the infant stimuli ($F_{1,5} = 22.48, p < .01, \eta^2_p = 0.82$). The effect of age was significant in the same condition ($F_{1,5} = 9.37, p = .02, \eta^2_p = 0.65$) but not in the different condition ($F_{1,5} = 2.45, p = .18, \eta^2_p = 0.33$).

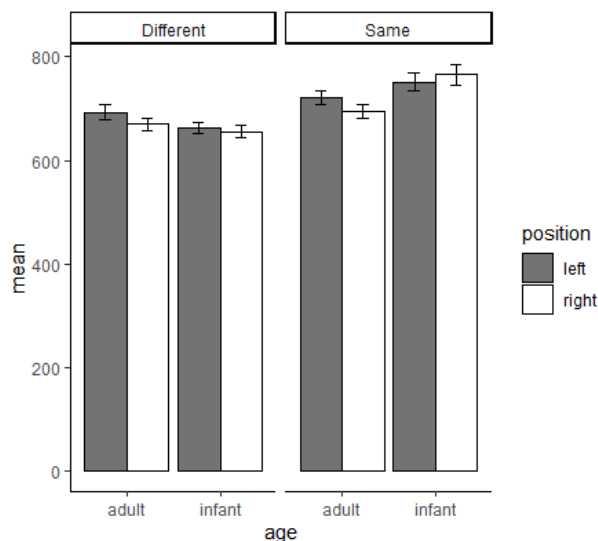


Figure 5. 3. The average response time in Experiment 2 (horizontal array). The error bars indicate the standard error.

As before, these results suggest that differentiating between faces from the same age category was more demanding than differentiating between faces from different categories (i.e., the significant effect of condition). In addition, it took more time for the chimpanzees to discriminate between two different infant faces than in the other conditions (i.e., the significant interaction effect of age and condition). I did not find any effect of the position of the target, including the interaction between position and age. Therefore, there was no evidence of correspondence between horizontal space and adult/infant faces.

5.3.2 Image Similarity Analysis

Figure 5.4 shows the differential score between each stimulus within each age category, which was calculated based on the SSIM. If this value is greater it means that there is a larger difference between the stimuli. This differential score was compared using the Mann-Whitney U-test. The results showed that there was no difference between the average similarity of the adult and infant stimuli among the same age category ($U = 106.5, p = .81$). The findings indicate that the physical variation in the stimuli within each age category was not significantly different between the adult and infant faces in terms of low-level features. It is therefore unlikely that the reason for the chimpanzees' asymmetric performance when differentiating between adult and infant faces is that the infant stimuli were more similar to each other than the adult stimuli.

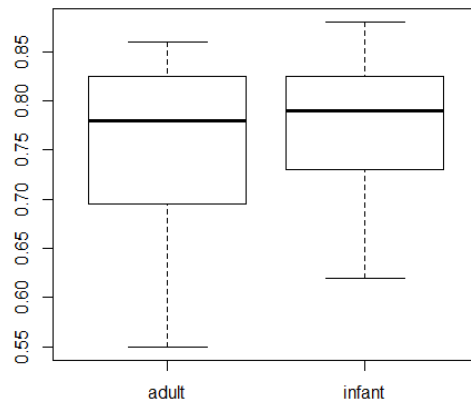


Figure 5.4. The boxplot presents the differential score between each stimulus within the age categories. The score was calculated based on the structural similarity index, and a greater mean value indicates that there is a larger difference between the stimuli. The statistical analysis found no significant difference between the adult and infant stimuli.

5.4 Discussions

The present study explored face processing related to age recognition from the aspect of a spatial mapping of face age in chimpanzees. The analysis of the performance and the response time indicated that there was no effect of position corresponding to the age category of the stimuli. That is, the results do not support the existence of the spatial representation of facial age in either a vertical (Experiment 1) or horizontal (Experiment 2) array in chimpanzees. The non-significant result of the correspondence between space and facial age imply some possibilities. Before proceeding the discussion, it should be noted that there is a possibility that the variation of the results among the relatively small sample size ($n=6$) may have masked the subtle effect if any. This is because in the horizontal array (Experiment 2) there was non-significant tendency (Figure A5.1). The response time tended to be slightly shorter in adult-right and/or infant-left condition in many participants. Thus it cannot be denied that a weak horizontal spatial mapping where an infant represented on the left and an adult represented on the right may exist in chimpanzees. Such modest spatial association may not be robust to any artifacts (e.g., individual's position bias). However, it should be considered carefully since the group analysis did

not find even approached significant interaction effect of position and age.

Otherwise, chimpanzees may not recognize faces as “adult” or “infant” as we do, in other words they may not extract conceptual age categories from faces. Previous studies have demonstrated that non-human primates also recognize a face image as representing face by reporting the neural activities which are selective for faces (e.g., Tsao et al. 2003, 2008). Moreover, the data of the present study indicates that the face discrimination performance differed between same condition versus different condition. It indicates that the faces across the different categories were perceptually more different compared with the faces within the same category for the chimpanzees. My previous study also shows that chimpanzees can differentiate adult faces and infant faces (Chapter 4). These evidence indicate that chimpanzees extracted shared visual features within each category. Therefore, the participants should have at least recognized that the stimuli I used were representing faces, which can be dissociated into two categories. However, for them that category may have not been based on age, but something else such as brightness.

The other possibility is that even though the chimpanzees extracted conceptual age category from face images they did not associate it with space for some reasons. Because what we know about time recognition in non-human primates are quite limited, it is difficult to conclude whether chimpanzees do not recognize the infant–adult in time sequence, or they do recognize it as related with time but not have a so-called mental timeline. Previous researches suggest that some time-related recognition in humans is shared with non-human primates. For example, *mental time travel*, in which one reconstructs past events and imagines the future, is partially shared with non-human primates (for review Suddendorf and Corballis 2010). However, how similar their time recognition is to humans is still unclear. This is because these studies have focused specifically on the aspect related to decision-making such as episodic memory or future planning, instead of testing time concept itself. Moreover, humans can easily imagine future or past decades, and spatial representation of time is also reported for

both types of images representing short and long periods of time (Fuhrman & Boroditsky, 2010). On the other hand, previous studies in non-human primates usually adopt a much shorter time window. Therefore, how non-human primates comprehend a longer time span, such as the recognition of another individual across decades from their infancy to adulthood should be examined.

Another finding of the present study is that our chimpanzees showed a faster response time when discriminating between adult faces than when discriminating between infant faces. These results did not occur because of the difference of physical similarities among the adult faces versus the infant faces since the image analysis showed that both were comparable. Human own-age bias is usually considered to reflect “more extensive, recent experiences with one’s own age group relative to other-age groups (Rhodes & Anastasi, 2012, p.146).” Similarly, this chimpanzees’ asymmetric efficiency in face processing probably arose because they were attuned to processing adult faces based on their daily face experiences. Our chimpanzees have experience of interacting with infants in the past but they had not seen infants for a while. On the other hand, they were living socially and interacting with other adult group members in their daily life. These asymmetric amounts of experiences of adult and infant conspecifics have likely led to the current results. This is probably not specific to our chimpanzees, but more general. Given that chimpanzee adults in general have more interactions with adults compared with individuals belonging to different age categories, it is likely that they have a superior face processing ability for adult individuals.

The current result is fully understandable in line with previous human studies that suggest the existence of the own-age bias. In our chimpanzees, extensive exposure to adult conspecific faces in their daily life likely have shaped their perceptual system toward expertise for adult faces. Nevertheless, in chimpanzees infantile face coloration may also be particularly responsible for the impaired discrimination performance. Chimpanzee infant faces are different from adult faces both in shape and color (Chapter 4). However, my previous study found that chimpanzees specifically pay attention to the

conspicuous infant face coloration, which is much paler color than adult one (Chapter 2 and 4). Therefore, it is possible that chimpanzees' attention was attracted to the unfamiliar face color (i.e. infantile face color) and their fluent face processing was distracted because of it. It is worth testing, then, which particular facial feature causes impaired face processing for infant faces in chimpanzees.

The present study has some limitations. First, it is challenging to interpret the null result of spatial mapping of face age only from the present study. As mentioned earlier, some possibilities remain. What I can tell from the results is that the positive evidence that chimpanzees were extracting the age concept from faces was not found, yet I cannot fully deny that possibility either. However, given that recognition of time concept in non-human primates has been seldom studied, the result can be a stepping stone for future comparative cognitive studies of time recognition including mental timeline. On the other hand, I found that chimpanzees show asymmetric performance for discriminating between adult faces and infant faces, which is seemingly similar to human own-age bias. Nevertheless, it is of note that I cannot conclude the efficient face processing for adult faces in our chimpanzees is the same phenomena to own-age bias in humans. This is because it is unclear whether chimpanzees of other age classes such as juveniles also show efficient face processing selectively for their cohort's faces. In order to understand whether this bias in chimpanzees is identical to the own-age bias in humans, a future study needs to examine this issue by using chimpanzees from a wider age range both as participants and as stimuli.

In conclusion, the present study explored two dimensions of facial age recognition in chimpanzees: spatial mapping and the effect of the different amount of experience. The current data did not support the existence of spatial mapping of the age categories in chimpanzees. However, I did find evidence of the superior processing of adult faces than of infant faces in adult chimpanzees. As far as I know, this is the first report of asymmetric face processing efficiency between infant and adult faces in non-human primates. This finding revealed a new aspect of chimpanzee's face recognition related with

age, which is seemingly similar to that of humans.

5.5 Tables

Table 5.1. Participant information.

Individual name (GAIN ¹ ID)	Sex	Age	Birth experience
Ai (0434)	Female	41	Parous
Ayumu (0608)	Male	18	-
Chloe (0441)	Female	37	Parous
Cleo (0609)	Female	18	Nulliparous
Pal (0611)	Female	17	Nulliparous
Pendesa (0095)	Female	41	Nulliparous

¹GAIN (the Great Ape Information Network) is the information network about Hominoidea living in Japan.

5.6 Appendix

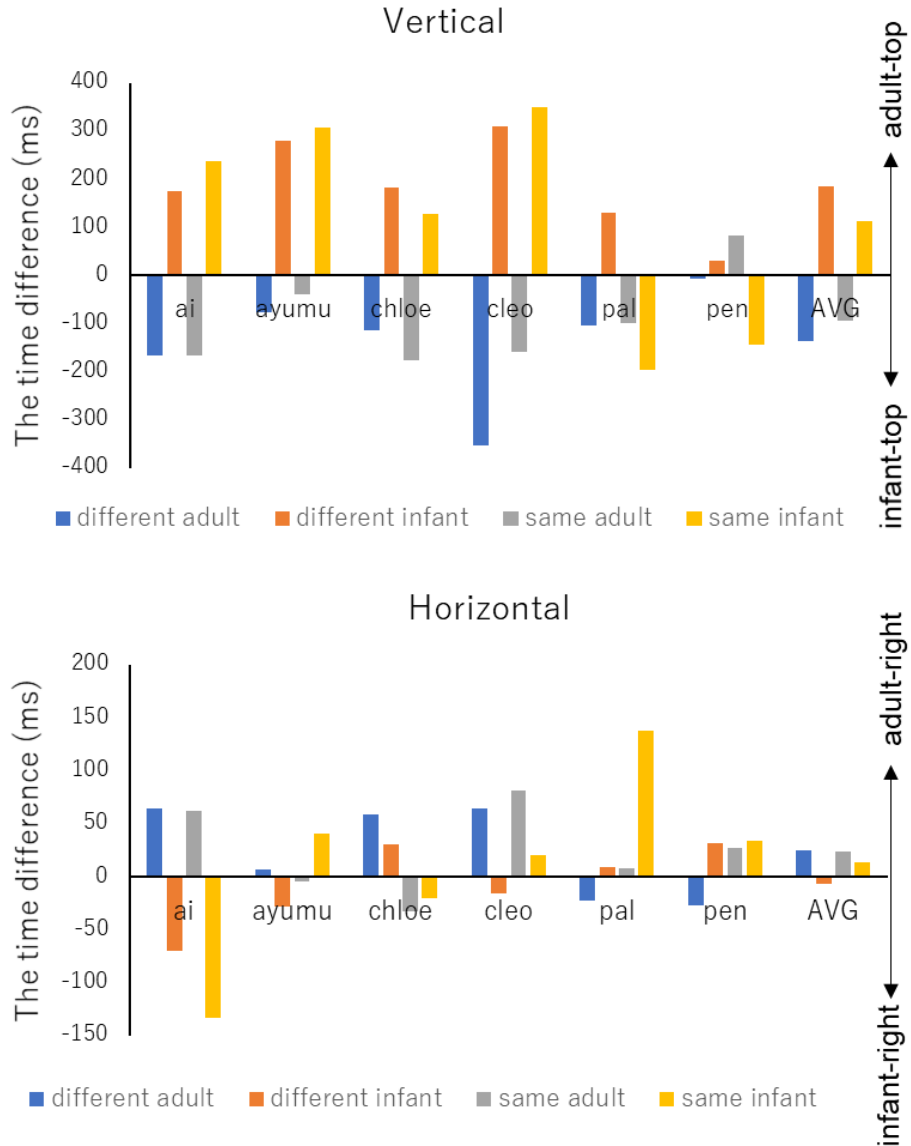


Figure A5.1. The individual data of the response time difference between top and bottom in vertical (Experiment 1) and left and right in horizontal (Experiment 2) for each condition.

Chapter 6: Impairment Effect of Infantile Coloration on Face Discrimination in Chimpanzees

6.1 Introduction

Humans extract various information about faces from facial color features (G. Rhodes et al., 2011). Likewise, non-human primates have a sensitivity to facial color. For example, species-specific facial color patterns play an important role in species discrimination, especially for some primate taxa at high risk of interbreeding, such as guenons (Allen et al., 2014; Winters et al., 2020). Facial color variation also exists among the same species, both across and within individuals. Previous studies demonstrated that monkeys show sensitivity to certain facial coloration, and it signals male physical quality or female pregnancy, which are both important in mate choice and social interactions (Gerald et al., 2009; Setchell et al., 2006; Waitt et al., 2003). Thus, facial coloration is an important cue in social judgements. Anecdotal reports raise the possibility that facial color variation among individuals also helps identification (Bradley & Mundy, 2008). This evidence of the high sensitivity to face coloration in non-human primates is consistent with an evolutionary hypothesis that one of the adaptive values of primates trichromacy is to extract information from face color variation (Changizi et al., 2006; Hiramatsu et al., 2017; Thorstenson, 2018).

Additionally, non-human primates are also sensitive to facial shape cues. For example, facial symmetry can indicate developmental stability (Rhodes et al., 1998), and it is also preferred by non-human primates (Paukner et al., 2017; Waitt & Little, 2006). Thus, comparative cognitive studies have investigated how each facial feature, facial color, and facial shape independently contributes to perception of social traits on faces (Koba et al., 2009, Chapter 4). Koba et al., (2009) found that macaques use both face properties to categorize sex for conspecific images. In their study, rhesus macaques were required to discriminate the sexes of the conspecific face stimuli. After the training, they

tested how monkeys respond to morphed face stimuli and found that monkeys used both shape and other characteristics for discrimination.

Potentially, age information can be extracted also from both facial shape and color features, at least in some primate species. A set of morphological features of infants, especially faces (e.g., relatively bigger eyes and forehead, small nose and mouth), is called “baby schema” (Lorenz, 1943). On the other hand, of approximately half of all primate species (Treves, 1997), infants have unique skin and/or coat coloration that differs from adults (Alley, 1980; Hrdy, 1976; Ross & Regan, 2000; Treves, 1997). Chimpanzee infants also have both unique facial color and shape characteristics (Chapter 4). Statistical image quantification of chimpanzee adult and infant faces revealed that infant faces have some baby-schematic characteristics (e.g., bigger eyes located lower in faces) and curved supraorbital torus, which contrasts with adults’ straight ones. Moreover, significant color differences also exist between adult and infant faces; infant faces have pale skin coloration, while adult faces have dark skin.

Although, how non-human primates perceive infant faces was not understood until recently, my previous study found that adult chimpanzees show worse face recognition performance toward infant faces compared to adult faces (Chapter 5). In the study, chimpanzees were required to match faces, including both adults and infants in an identical matching-to-sample task. As a result, the response time was consistently longer in discriminating among infant faces than among adult faces. This indicates that adult chimpanzees were better at discriminating adult faces than infant faces. The reason for this asymmetric performance in chimpanzees is unknown, but their infantile face coloration may be particularly responsible for the impaired discrimination performance. My previous studies have demonstrated that infantile face color is a particularly salient feature for chimpanzees. The eye-tracking study revealed that chimpanzees’ spontaneous attention is attracted to infantile facial coloration (Chapter 2). Infantile coloration serves as a more robust cue to age perception than a facial shape cue in chimpanzees (Chapter 4). Such salient and unfamiliar face features may distract chimpanzees’ fluent

face processing by grabbing their attention.

The aim of the present study is to investigate the impairment effect of infant face coloration. As illustrated above, chimpanzee infant faces are significantly different from adult faces in facial shape and color dimensions (Chapter 4). Therefore, it is theoretically possible that discrimination difficulty for infant faces is induced solely by facial color or shape, or by a combination of both. Applying the same morphing technique used in the previous study (Chapter 4), I created four types of face stimuli by independently manipulating shape and color: (1) faces with adult shape and adult color, (2) faces with adult shape with infant color, (3) faces with infant shape and adult color, (4) faces with infant shape and infant color. I compared face identification performance in a face matching task across four face stimulus conditions and tested which facial color and shape has the greater effects on the difficulty of face identification. Since a previous study has found that chimpanzees have higher sensitivity to face color than shape cues related with age difference, I predicted that face color of infant faces would contribute more to discriminability than face shape in chimpanzees.

6.2 Methods

6.2.1 Participants

Six adult chimpanzees took part in the experiment (five females, aged 18–42 years). The participants voluntarily came to the experimental booth (1.8 m × 2.15 m × 1.75 m) and joined the experiment. During the experiment, they were not restrained and could quit the experiment whenever they wanted. The chimpanzees lived socially in the Primate Research Institute, Kyoto University. All participated in the study using morphed stimuli of adult and infant faces (Chapter 4) and the other showing superior face processing for adult faces over infant faces (Chapter 5). The chimpanzees lived in an enriched environment, which featured both an indoor and an outdoor enclosure, and they had free access to water and received food (fresh fruits, vegetables, sweet potatoes, and nutritionally balanced

biscuits) several times each day. All research procedures followed institutional guidelines (Primate Research Institute 2010 version of “The Guidelines for the Care and Use of Laboratory Primates”), and the experiment protocol was approved by Animal Welfare and Animal Care Committee of the Primate Research Institute (2020-193) and the Animal Research Committee of Kyoto University.

6.2.2 Apparatus

The experiment was conducted in an experimental booth (1.8 m × 2.15 m × 1.75 m). A matching-to-sample task was conducted using a 17-inch touch-sensitive LCD monitor (IO Data LCD-AD172F2-T, 1280 × 1024 pixels), and a universal feeder delivered food reward (Biomedica, BFU310-P100). Stimulus presentation, response detection, and feedback were controlled by a customized program written in Microsoft Visual Basic 2010 Express working on a personal computer (CPU: Core [TM] i3-4130 3.40 GHz; Intel, Santa Clara, CA).

6.2.3 stimuli

I generated four types of morphed stimuli with Webmorph (version v0.0.0.9001): (1) faces with adult shape and adult color, (2) faces with adult shape and infant color, (3) faces with infant shape and adult color, (4) faces with infant shape and infant color (Figure 6.1). These morphed faces were generated from eight adult and eight infant faces (four female and four male faces for each), which were used in Chapter 4, and facial shapes were represented by 118 landmarks according to the previous study. Original images depicted images aged 2 to 10 months and adults aged 13 to 22 years old at the time the pictures were taken. To make a set of “age-neutral” faces, one infant face and one adult face chosen at random were superimposed, resulting in eight age-neutral faces (Figure 6.1). Each original image was used only once. The age-neutral images were transformed either 50% adultized or 50% infantilized for shape and color dimension, resulting in four types of faces with adult or infant shape score and color score. I prepared eight stimuli for each condition. Importantly, eight faces have some physical variation

within each condition, but the difference among them was the same among four conditions.

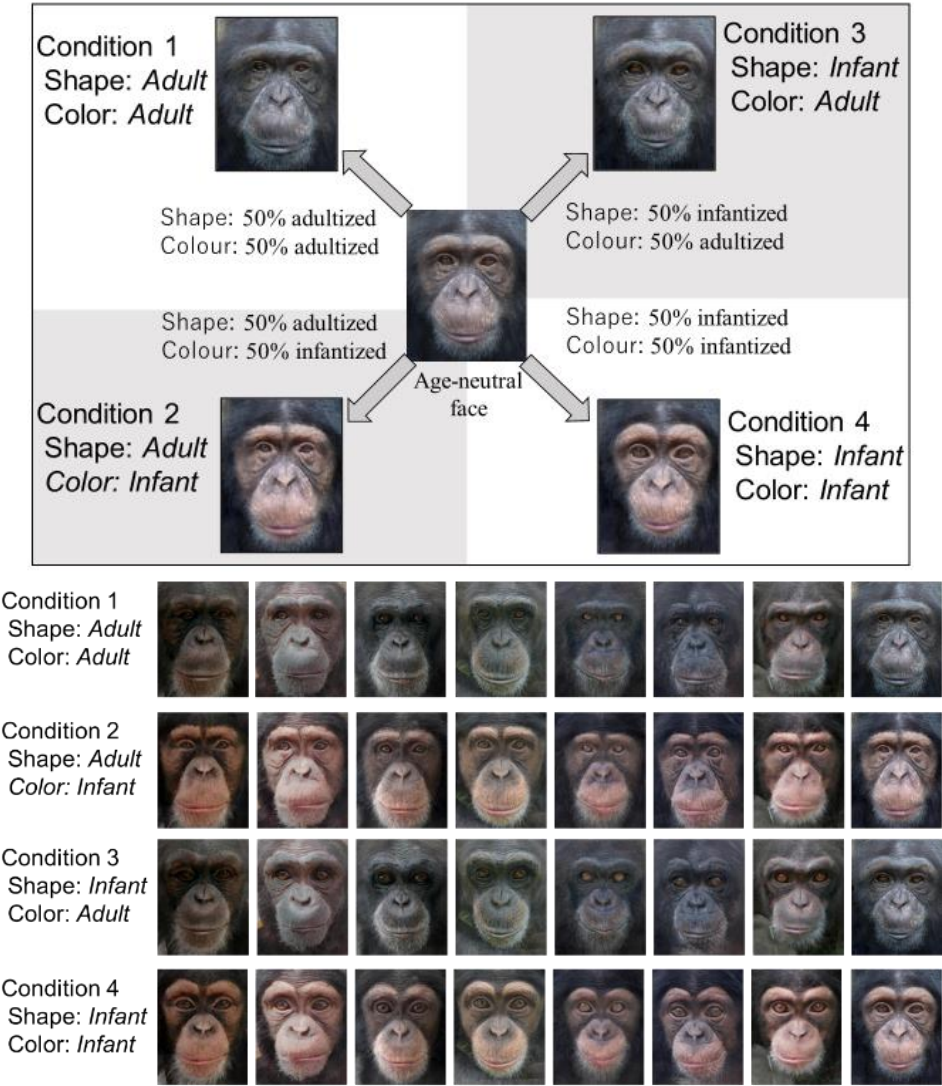


Figure 6.1. Morphed stimuli. Sample stimuli and comparison stimuli were constantly assigned from the same condition.

6.2.4 Procedures

I conducted an identical matching-to-sample task (Figure 6.2). In the task, each trial started immediately after the participant touched a start key. The start key appeared twice; horizontally in different places at the bottom of the monitor, and the second was always presented in the center. Once

the participant touched the start key, a sample stimulus appeared at the center of the monitor for 500 ms. Then, it disappeared and two comparison images were presented. One of the comparison images was identical to the sample stimulus, and the other was the face with different identity selected from the same shape and color manipulation condition. The participants were required to touch the identical image as the sample. When they chose the correct answer, a food reward (a piece of apple) and chime sound were delivered. When they chose the wrong answer, no food reward was delivered, and a different sound was played. During a session, the trial order of the condition and the stimuli was pseudo-randomized. There were 56 combinations of the two comparison images. For each combination, there were two arrangements (left or right), resulting 112 unique trials for each of the four conditions. The total 448 unique trials were divided into 8 sessions and repeated four times. One session consisted of 56 trials, and two sessions were completed each day.



Figure 6.2. Matching-to-sample task.

6.2.5 Analysis

The accuracy and response time were analyzed with a generalized linear mixed model (GLMM) to test whether the shape and color of the stimuli significantly affect face recognition performance. All the analyses were conducted on R 3.5.1 (R Core Team, 2018) with the “lme4” package (Bates et al., 2015). For the accuracy the answer on each trial (correct versus incorrect, coded 1 or 0, respectively) was included as a response variable, and the shape of the stimuli (adultized or infantized),

the color of the stimuli (adultized or infantized), and their interaction were included as explanatory variables. I used a binomial distribution for the accuracy. The random effect of the participant and session number for the color, the shape, and the interaction of them were included. In addition, the response time was analyzed in the same way as the accuracy, except that gamma distribution was applied. Only data from correct trials were analyzed. The response times that exceeded the mean plus 3 SDs (i.e., 2,626 ms) were excluded from analysis, resulting in 9.79% of the data being discarded.

6.3 Results

Figure 6.3 shows the mean accuracy and the mean response time for each condition (see also Figure A6.1 for individual data). For the accuracy, the results revealed a significant main effect of color (Estimate = -0.35, standard error (SE) = 0.17, z = -2.07, p = .04, 95% confidence interval (CI) [-0.68, -0.02], Table 6.1), while neither the main effect of shape (Estimate = -0.007, SE = 0.11, z = -0.07, p = .95, CI [-0.23, 0.22]) nor the interaction effect between color and shape (Estimate = -0.02, SE = 0.21, z = -0.10, p = .92, CI [-0.42, 0.38]) were significant. The face identification is disrupted 3.6% greater in the infant color condition than in the adult color condition, on average. For the response time data, the results showed a significant main effect of color (estimate = -0.05, SE = 0.02, t = -2.22, p = .03, CI [-0.10, -0.01], Table 6.2), while neither the main effect of shape (Estimate = -0.03, SE = 0.03, t = -1.1, p = .27, CI [-0.08, 0.02]) nor the interaction of them (Estimate = 0.04, SE = 0.03, t = 1.23, p = 0.22, CI [-0.02, 0.11]) were significant. The response time is increased by 18 ms in the infant color condition compared with the adult color condition, on average.

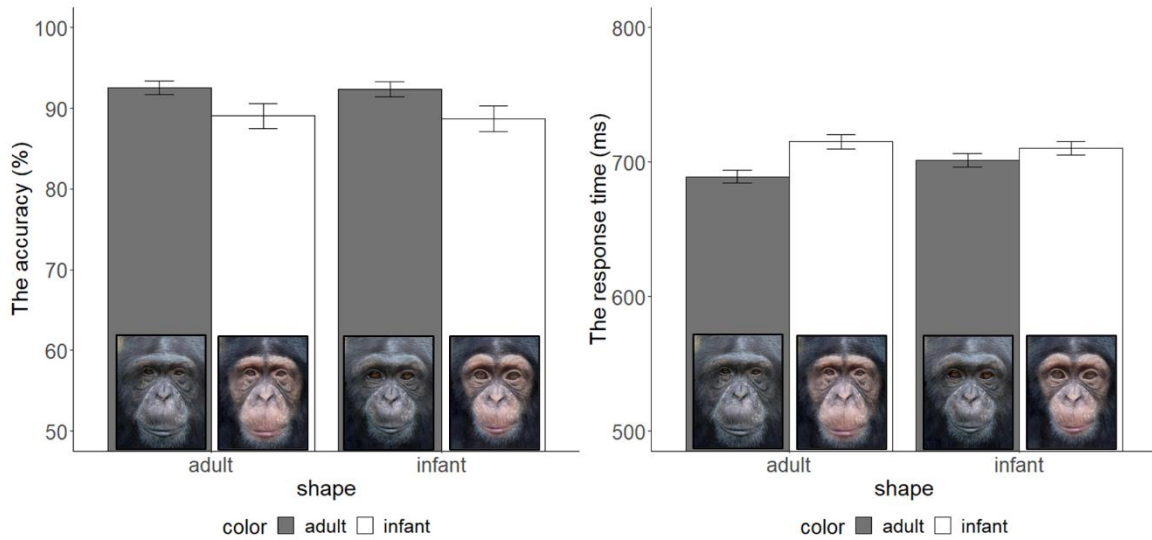


Figure 6.3. Accuracy (left) and response time (right). The error bar indicates the standard error.

6.4 Discussions

The present study investigated the impairment effect of infantile coloration on face discrimination in chimpanzees. As predicted, the results showed that chimpanzees made more mistakes and took a longer time when asked to match the face with infant coloration regardless of the face shape. This indicates that the infant facial color, rather than facial shape, impairs face recognition in chimpanzees. This study is the first to demonstrate the interference effect of infantile face coloration on face recognition in non-human primates. The different performances among conditions are not due to low-level visual confounds of the stimuli. Rather, physical differences among stimuli remain the same among four conditions due to the controlled way of creating the stimuli. Therefore, if chimpanzees had matched faces based solely on physical differences between the given two stimuli, their performances would have not differed among the conditions. Moreover, my previous study has demonstrated that both shape and color differences are robust between adult faces and infant faces in chimpanzees (Chapter 4). Furthermore, the novelty of the stimuli unlikely explains these results either. If novelty, the lack of experience, simply affects the results, chimpanzees would have shown worse performance for the face

stimuli with adult color and infant shape and for the face with infant color and adult shape, because participants have never seen such “incongruent” faces before. However, the congruency of the stimuli does not explain the performance, because there was no effect of face shape on the matching difficulty.

Then, why does infantile face coloration make face recognition difficult? Asymmetric recognition efficiency among face categories is known in humans. For example, efficient face processing is observed for own-race or own-age faces compared with other-race or other-age faces (Chance et al., 1986; Meissner & Brigham, 2001; Wright & Stroud, 2002). One of the explanations of such phenomena is based on the amount of experiences. That is, frequent exposure to certain face types results in the acquisition of *face schema*, a face prototype, and faces that deviate from this schema are processed less efficiently (Goldstein & Chance, 1980). Alternatively, the asymmetric face processing efficiency was explained by Sporer's in-group/out-group model (IOM) of face processing (Sporer, 2001). According to this model, an in-group face is automatically processed with configural coding, which is characteristic of expert processing of normal upright faces. In contrast, an out-group face is first categorized as out-group, triggered by a perception of characteristic cues before more typical face processing. Hence, IMO is independent from the experiences and applicable to the processing strategies of both certain race and age groups faces (Anastasi & Rhodes, 2005). It is difficult to conclude which of them, experience or the other factor, explains the results of this study, and it is possible that both are related to these results. Nonetheless, once chimpanzees categorize an infant face as an “atypical face” or “out-group face” by its striking coloration, more detailed usual face processing may not continue in an equivalent manner to a “usual” adult face. The previous studies found that infantile face coloration attracts chimpanzees' attention (Chapter 2 and 4). Chimpanzees' fluent face recognition may be disrupted by unfamiliar and salient (e.g., infantile) face color.

The current results do not contradict “the paternity cloak hypothesis” (Treves, 1997), which assumes that infant coloration makes identity and paternity detection difficult. Treves proposed that the

unique natal coat color might prevent males from identifying phenotypic markers signaling paternity based on physical appearance, leading to reduced infanticidal risk. The current study is not testing the paternity cloak hypothesis. Infantile coloration makes chimpanzees' face identification less accurate and slightly less immediate, but it is unclear whether particular visual cues, which are important for kin recognition, if any, are also masked by the coloration. Moreover, testing the adaptive function of infantile face color in evolution is challenging. Nevertheless, it may be possible that infantile face color makes the identity and potential paternity of chimpanzee infants difficult to detect in the wild. In this regard, the variations among species or sub-species of genus *Pan* are worth noting. Infantile facial coloration exists in chimpanzees, but not (or much less conspicuous) in bonobos. Moreover, the conspicuousness of infantile coloration varies even among subspecies of chimpanzees (Napier & Napier, 1967). In the present study, both the participants and the individual depicted in original images of the stimuli were western chimpanzees. Future studies should use species with more conspicuous and less conspicuous infantile coloration (i.e., eastern chimpanzees and bonobos) as both participants and stimuli.

Despite the novel findings, there are some limitations that future studies should consider. First, it remains to be seen whether infant face coloration particularly makes face recognition more difficult as compared with any unfamiliar face coloration. Studies should test whether other unrelated coloration makes face recognition difficult. Second, it remains unclear whether the interference effect of chimpanzee's infantile face coloration is specific to conspecifics. Future studies should test whether other species (e.g., humans) show similar results. If the impaired effect of infantile coloration on chimpanzees' face recognition results from the asymmetric amounts of experience between adult and infant faces, humans with less experience of chimpanzees (both adults and infants) will not show the same effect. However, chimpanzee experts who have regular experiences with adult chimpanzees will show similar results to chimpanzees. Furthermore, it is unclear whether this phenomenon is applicable to only chimpanzees, any primate species with conspicuous infantile coloration, or primates in general.

Hence, other primate species, including species with and without conspicuous infantile coloration, should be tested similarly. Even though the above limitations exist, this study is the first to demonstrate the robust impaired effect of infantile face color on discriminability. The independent role of each of facial property has not been examined well in non-human animals. A comparative cognitive approach like this study will shed light on the different and shared face recognition mechanisms between humans and non-human animals.

6.5 Tables

Table 6.1. The results of GLMM analysis for accuracy

<i>Factor</i>	<i>Estimate</i>	<i>SE</i>	<i>Z</i>	<i>p</i>	<i>95 % Confidence Interval</i>
Intercept	2.55	0.13	20.35	<.001	[2.30, 2.79]
Color	-0.35	0.17	-2.07	.04	[-0.68, -0.02]
Shape	-0.007	0.11	-0.07	.95	[-0.23, 0.22]
Color * Shape	-0.02	0.21	-0.10	.92	[-0.42, 0.38]

Table 6.2. The results of GLMM analysis for response time

<i>Factor</i>	<i>Estimate</i>	<i>SE</i>	<i>t</i>	<i>p</i>	<i>95 % Confidence Interval</i>
Intercept	1.48	0.07	22.35	<.001	[1.35, 1.61]
Color	-0.05	0.02	-2.22	0.03	[-0.10, -0.01]
Shape	-0.03	0.03	-1.10	.27	[-0.08, 0.02]
Color * Shape	0.04	0.03	1.23	0.22	[-0.02, 0.11]

6.6 Appendix

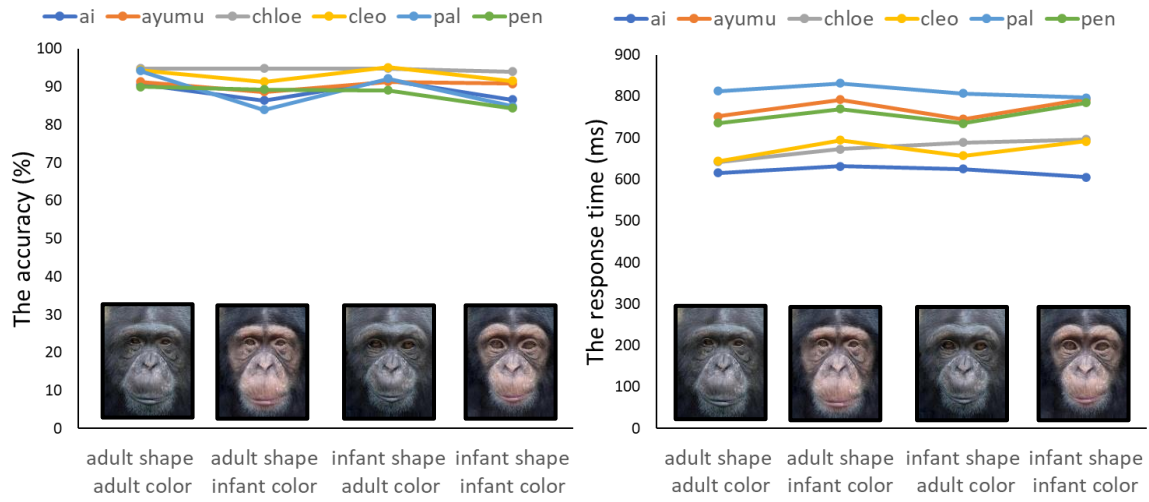


Figure A6.1. Individual data for accuracy (left) and response time (right).

Chapter 7: General Discussions

7.1 Summary of the findings

The aim of this thesis was to reconstruct the evolutionary pathway of humans' recognition of infant faces and test universality and uniqueness of a primary infant face cue in primates. For this aim I investigated how great apes respond to infant face features from three aspects. First, I studied visual attention to infants in naturalistic images in two species of great apes. I found that chimpanzees, but not bonobos, show visual preference for infants. Second, I investigated primary cue in face discrimination between infants and adults and within age categories in chimpanzees. I found that the specific color, but not the shape, is the primary facial cue of infants in chimpanzees. Finally, I investigated whether chimpanzees represent a conceptual age category from faces. The results did not provide positive evidence for this question. The main finding of this thesis is that each species has species-specific characteristics of infants and ways of responding to them. Previous studies suggest that human infants attract adults due to baby schema, facial shape features. On the other hand, chimpanzee infants attract adult attention due to unique face coloration. Meanwhile, bonobo infants do not appear to have particular facial characteristics that capture the attention of adults. This thesis calls for reconsideration of the idea that baby schema has general effect across species.

Summary of each chapter

The first parts of the thesis investigated the great apes' spontaneous looking behavior to adult and infant faces of conspecifics and other species (Figure 7.1). Chapter 2 revealed that chimpanzees looked at infant faces of conspecifics for longer duration than adult faces. However, such preference for infants was not observed for other species. Importantly, the visual preference for infants in chimpanzees disappeared when facial coloration was matched between conspecific infants and adults. Conversely, bonobos did not show visual preference for infants of any species. The results indicate that the species differences exist in visual preference for infants. Although chimpanzees looked at conspecific infants

for a longer time, it is unclear whether such visual preference was based on parenting motivation or something else. Therefore, Chapter 3 examined how chimpanzees' and bonobos' eye gaze at infants is affected by OT (oxytocin), a hormone which regulates parenting behavior. However, as a result, the looking time of both species at infant and adult faces was not significantly changed by OT administration. Further study is needed before interpreting the motivation of great apes' looking behavior to infants.

The second half of the thesis focused on chimpanzees face recognition of infants versus adults and the role of facial features. The results showed that infant face coloration in chimpanzees attracts attention from conspecifics. However, it was unclear whether chimpanzees use it as a cue to discriminate between adults and infants. Therefore, Chapter 4 tested whether chimpanzees can discriminate between adult and infant faces and further examined the relative contribution of facial color and shape on categorization. I trained chimpanzees to discriminate between adult and infant faces and tested the generalization to the morphed stimuli with independently varied color and shape features. As a result, at least three chimpanzees successfully discriminated adult faces and infant faces. Moreover, although image analysis found significant differences between adult faces and infant faces in both shape and color, face coloration rather than face shape served as cues for discrimination. Although I found that chimpanzees could discriminate between adult faces and infant faces, it was unclear whether they represent the abstract age category from faces. Therefore, Chapter 5 examined whether chimpanzees are doing this by testing spatial mapping of adult and infant faces. As a result, I could not get the positive evidence that chimpanzees extract conceptual age categories from face images. However, I found that face matching performance was better for adult faces than infant faces. This may be because, for our chimpanzees, and probably adult chimpanzees in general, the frequency of the exposure to adult faces is higher than exposure to infant faces. In Chapter 6, I further investigated the impairment effect of infantile face color versus shape in face recognition. I conducted an identical matching-to-sample task and compared the performance among four conditions with facial color and shape were either adult or

infant respectively. I found that the color, but not the shape, of infant faces makes the face recognition difficult in chimpanzees. This result confirmed the saliency of infantile face coloration in chimpanzees and further suggested the impairment effect of infantile face color in face discrimination. Chimpanzees' usual and fluent face processing does not proceed due to such salient face feature.

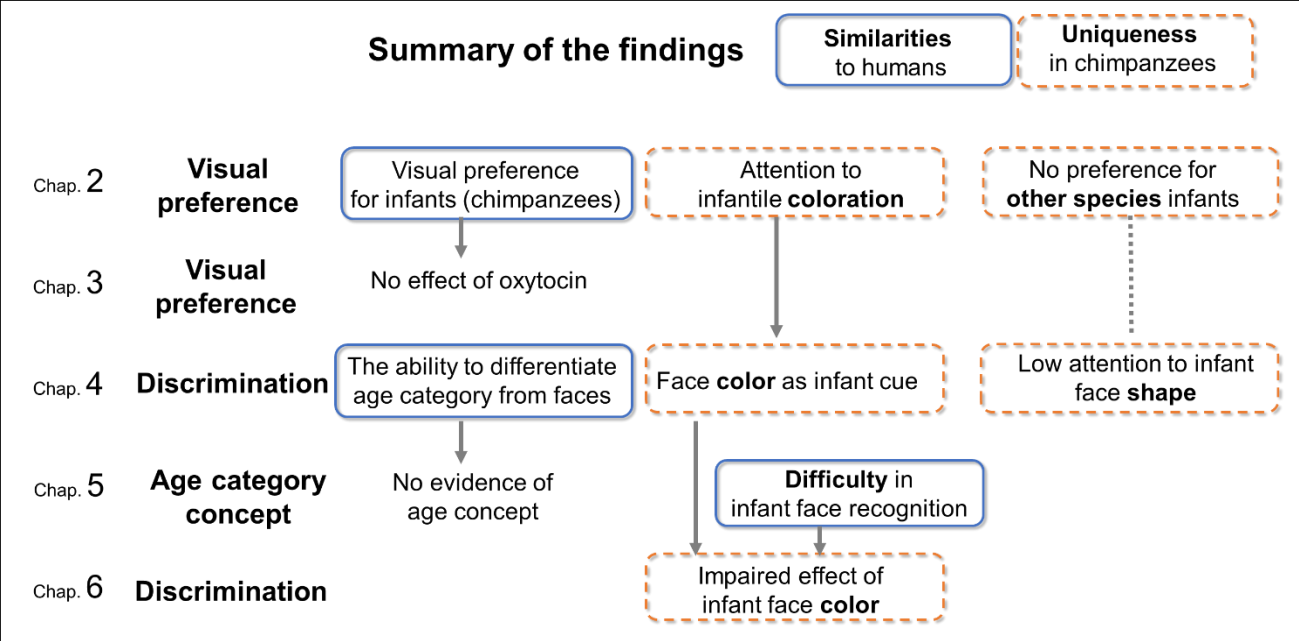


Figure 7.1. Summary of the findings

7.2 Baby schema effect may not be universal

7.2.1 Face color serves as infant cues in chimpanzees

The results from great apes were different from what has been reported in previous human studies on two points. First, great apes did not show visual preference for infants of other species. Second, the primary cue of an infant face for chimpanzees was not face shape but face color. In humans, the effect of baby schema has been the center of discussion. For understanding human recognition of infant faces, it is probably effective to focus on baby schema, because humans do not have conspicuous infantile coloration (although infants typically have brighter skin than adults in humans too, Fluhr et al.,

2000). However, in chimpanzees, I found that the infantile characteristics other than baby schema, specifically species-specific color and shape features, exist, and chimpanzees pay more attention to species-specific color. In my previous study (Kawaguchi, unpublished), when presented with a pair of conspecific faces with “high baby schema” and “low baby schema,” chimpanzees were not sensitive to shape differences by their looking time. This contrasts with humans, who have high sensitivities to baby schema. For humans, most conspicuous infantile face characteristics may be the face shape, while for chimpanzees it is the facial color. Importantly, this explains, at least in part, why humans have preference for infants of other species (Golle et al., 2015; Little, 2012; Maestriperi & Pelka, 2002), while chimpanzees do not (Chapter 2). Human perception of “babyhood” can be easily generalized to other species, probably because humans have high sensitivity to infantile face shape, which is widely shared with infants of various species. However, chimpanzees pay attention to their species-specific infantile coloration, so they did not show visual preference for infants of other species, which do not have the same infantile color. Nonetheless, it remains unclear whether chimpanzees’ tendency to attend color features instead of shape features is a context-specific characteristic regarding age-related face processing or a more general visual characteristic. It can be tested by using types of stimuli other than faces as well.

Since proposed by Lorenz (1943), it has been thought that baby schema exists across species and induces parenting motivation in humans and non-human animals. Image analysis in Chapter 4 suggests that some features characterized by the baby schema exist in chimpanzees. However, the results of this thesis contradict the view that the baby schema effect is universal across species, which provides awareness to consider species differences of infant appearance and adults’ sensitivity to the appearances. This does not conflict my previous study of capuchin monkeys (Kawaguchi, Kuroshima, et al., 2019), where monkeys were trained to categorize adult and infant faces. After the training, the learned categorization spontaneously transferred to novel stimuli of the same species but did not transfer to

novel stimuli for other species. The result indicates that monkeys used species-specific features instead of species-common features for categorizing adult and infant faces. Thus, even though we share some infant visual characteristics, attention weighting varies among species.

7.2.2 How humans acquired high sensitivity to baby schema?

As a result of studying great apes and comparing the findings with human previous studies, it appears humans' high sensitivity to and preference for baby schema has been acquired after evolving from the common ancestor of humans and genus *Pan*. Even if infantile shape features, such as baby schema, are shared across taxa (which is assumed but must be tested with wider species), it is possible that it may merely reflect developmental physical restrictions without psychological functions for many species. Humans may have uniquely developed the strong preference for baby schema, though the reason is unknown. Developing high sensitivity and strong preference for infantile features may have been adaptive for humans, who have an extensive cooperative breeding system for rearing altricial infants.

It is unclear why, for humans, the primary cue of infants is baby schema but not conspicuous infantile coloration as is for chimpanzees. However, it is possible that infantile coloration and baby schema may differently affect perceivers. Perceiving infantile coloration might be done at a glance, requiring a simpler processing, while perceiving baby schema might require more configural processing, because the relative size of facial parts is recognized in the context of the whole face (Hodsoll et al., 2010). It is assumed that processing on simpler features (e.g., skin tone) precedes complex configurations (e.g., relative size of eyes) (Hodsoll et al., 2010). Thus, two infantile features may affect perceivers differently. For example, infantile coloration may primarily function as defining an individual as an infant, while baby schema may primarily function as conveying further information (e.g., health or age) after categorizing as an infant. The infant appearance and adults' sensitivity to it in each species may be, at least in part, determined based on ethological factors of the species, such as the existence of

infanticide or the extent of alloparenting.

There is a possibility that high sensitivity to baby schema may not be universal even within humans. It is pointed out that majority of current psychological studies are conducted with people from “Western, educated, industrialized, rich, and democratic (WEIRD)” societies (Henrich et al., 2010), and this applies to psychological studies on human recognition of infant faces. Thus, it is questionable whether a limited sample of modern people represent all humans well. For example, it is famous that medieval paintings draw children as “small adults” lacking baby schematic features, which suggests that people in that era may not have considered an infant as adorable due to specific morphological features. Additionally, a pilot study with Malaysian people suggested the possibility that comparatively bigger eyes, which is one of the characteristics of baby schema, may not make a face look younger for people in certain societies (Kawaguchi, unpublished). Thus, humans in other eras or societies may not recognize infants in the same way as participants of current psychological studies. It is impossible to test humans in past eras, but it is possible and important to test humans of various societies.

7.3 Comparative cognitive approach to recognition of infant faces

Although the findings highlighted the difference in primary infant face cues between chimpanzees and humans, some basic face processing that occurs when people are looking at infants were found in chimpanzees too, which should not be underestimated. First, visual preference for infants was observed in chimpanzees (Chapter 2). Second, chimpanzees can discriminate between adult and infant faces (Chapter 4) like for humans (M. G. Rhodes, 2007), and capuchin monkeys (Kawaguchi, Kuroshima, et al., 2019). Various cues besides faces should be available for the age category in the wild. Nevertheless, my results indicate that chimpanzees can extract shared face features within each age category. Third, the difficulty of recognizing infant faces for adult individuals is shared between humans

and chimpanzees (Chapter 5). Besides humans, this is the first report of asymmetry of face processing performance between adult and infant faces. My studies suggest that visual preference for infants and face discriminability between and within age category are shared with chimpanzees, even though the cues they use are different from humans.

This thesis adopted comparative cognitive approaches and found both similarities and differences among species. Although in this thesis I did not make direct comparisons between humans and great apes, it is ideal to test humans in different societies and non-human animals in a similar approach. Many previous human studies on infant face recognition are based on verbal reports (e.g., “How cute/attractive is this?”) (Kawaguchi et al., in press). This method may be difficult to apply to people with a different language system and definitely impossible to apply to non-human animals. Moreover, self-reporting is also susceptible to social desirability-bias to indicate a preference for infants, especially in female participants (Charles et al., 2013; Maestriperi & Pelka, 2002). Methods, like the ones used in this thesis, such as eye-tracking task or touch-panel task, provide more objective data and are applicable not only to great apes but also to other animals and humans. Testing multiple species, including humans, on an equal footing will shed further light on whether a certain infantile feature and response to it has been conserved across species or uniquely evolved in certain species.

7.4 Future directions

There are some limitations and intriguing research questions that this thesis did not cover and future studies should address. First, in this thesis I used only visual stimuli, especially face stimuli. However, Chapter 5 failed to find evidence that chimpanzees extract age category concepts from faces. Therefore, I cannot conclude whether chimpanzees recognize faces as “adult faces” and “infant faces” like humans. Future research can address this point by using multiple types of infant stimuli. Cues other than from the face, such as body size, body movement, auditory cues, olfactory cues, should be available,

and they likely play some roles in recognizing infants. Using multiple types of infant stimuli will make primates' age concept testable through association of multimodal cues. Using auditory stimuli may be promising because infant vocalizations have unique characteristics. For instance, exposure to infant vocalization increases the responsiveness to infants in male common marmosets (Barbosa & da Silva Mota, 2014). The acoustic structure and function (i.e., attracting caregiver's attention) of an infant distress call is conserved across mammals (Lingle et al., 2012). Therefore, such infant vocalization may be fundamental and ethologically relevant cues in various species, including great apes. Using visual and auditory cues of infants can test whether great apes have a concept of infant and adult beyond categorization of physical similarities.

Second, this thesis tested visual preference (Chapters 2 and 3) and discriminability (Chapters 4–6) for infant faces, but it could not test the appraisal of infant stimuli, including cuteness perception in humans. Examining the valence of the stimuli for non-human primates is challenging, if not impossible, but needed in order to understand the motivational mechanisms of their affiliative and agonistic behaviors toward infants. Chapter 3 tried to examine the valence of infant stimuli for apes by testing the effect of hormonal administration; unfortunately, it remains unclear from this study. Studying the valence of infant stimuli makes it possible to draw a whole picture of cognitive mechanisms underlying various behaviors toward infants, both positive and negative. As previously mentioned, infant stimuli are usually preferred by humans and enhance parenting behavior. Meanwhile, in humans, cognitive mechanisms that may be related with negative behavior toward infants, such as abuse or neglect, was studied. For example, specific neural activity, which is implied in caregiving, is observed when people are looking at normal infant faces but is diminished when looking at infant faces with small abnormalities (e.g., cleft lip) (Parsons et al., 2013) or low baby schema (Glocker, Langleben, Ruparel, Loughhead, Valdez, et al., 2009). This may reflect the negative side of humans' high sensitivity to infantile face morphology, and it may cause disruption of or low-quality caregiving for infants. Studying

cognitive mechanisms of negative behavior toward infants in primates is important for non-human primates as well, since infanticide is observed in a certain number of the primate species.

One potential way to interpret the meaning of “infants” for chimpanzees should be to check the impact of participants’ demographic factors (e.g., sex, age, maternal experience) on their response toward infants. In chimpanzees and bonobos, mothers are primary caregivers, as in most other primate species. In humans, many studies have reported the gender differences of visual preference for infants; females, compared to males, are more motivated to look at infant faces (Cárdenas et al., 2013; Charles et al., 2013; Hahn et al., 2013). Meanwhile, males kill more than females do, including infanticide in chimpanzees (M. L. Wilson et al., 2014). Thus, it could be possible to understand apes’ motivation of visual interest in infants if gender differences are discovered. However, the visual inspection of the results of our chimpanzee participants especially in Chapters 2 and 3 did not find such systematic tendency. Further studies should be conducted, ideally with larger sample sizes to test the effect of participants’ attributes.

The effect of individual attributes should be considered for the stimuli as well. Individuals have multiple layers of attributes besides age. An “infant” can also be a “group member,” “female,” or “my offspring,” simultaneously. It can be expected that great ape responsiveness is higher toward their own infants compared with unrelated infants, as it is in humans. Primate response may vary depending on the sex of infants. For example, in chimpanzees, males are dominant sex and remain in the natal group, while females are subordinate and migrate when they mature. Moreover, male chimpanzee infants are at a higher risk of infanticide than female infants are (Hiraiwa-Hasegawa & Hasegawa, 1994). The impact of infant’s attributes and the perceiver’s attributes should be tested in future studies.

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