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Cognitive Development 20 (2005) 49–63

COGNITIVE DEVELOPMENT

Development of face recognition in infant chimpanzees (*Pan troglodytes*)

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Abstract

In this paper, we assessed the developmental changes in face recognition by three infant chimpanzees aged 1–18 weeks, using preferential-looking procedures that measured the infants' eye- and head-tracking of moving stimuli. In Experiment 1, we prepared photographs of the mother of each infant and an "average" chimpanzee face using computer-graphics technology. Prior to 4 weeks of age, the infants showed few tracking responses and no differential responses. Between 4 and 8 weeks of age, they paid greater attention to their mother's face. From 8 weeks onward, they again showed no differences, but exhibited frequent tracking responses. Experiment 2 investigated the infants' tracking responses between a familiar human's and an "average" human face. The infants did not show any evidence of recognizing the human faces. We discuss the development of face recognition in relation to the effects of other species' faces and postnatal visual experience.

Keywords: Face recognition; Infant chimpanzees; Development; Mother's face; Human face

1. Introduction

From their birth, infants appear to preferentially look at faces. Studies on the development of face/non-face discrimination in human infants, using visual preference techniques,

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0885-2014/$ – see front matter
doi:10.1016/j.cogdev.2004.12.002

demonstrated that newborns preferentially track face-like patterns over non-face patterns (e.g., Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; Macchi Cassia, Simion, & Umiltà, 2001).

Johnson (1990) suggested that a subcortical visual pathway involving the superior colliculus controls the tracking of moving face-like stimuli in the first month. Johnson and Morton (1991) applied the term "CONSPEC" to this primary mechanism. CONSPEC operates from birth and its functioning rapidly declines within 1 month. A second mechanism, which they named "CONLERN," was thought to be acquired at around 6–8 weeks of age. Johnson and Morton (1991) proposed that there was a developmental shift in processing from the subcortical visual pathway to the second mechanism that appears in plastic cortical visual pathways. This second mechanism is thought to enable the recognition of individual faces.

On the other hand, some studies have demonstrated that 4-days-old neonates look longer at their mothers' faces than at a stranger's face (e.g., Bushnell, Sai, & Mullin, 1989; Field, Cohen, Garcia, & Greenberg, 1984; Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grent, 1995). Namely, these evidences are not consistent with Johnson and Morton's (1991) two-process theory of face recognition. According to their theory, only 6–8 week and older infants would be able to recognize individual faces (CONLEAN), because this ability relies on the cortical systems that are not functional by 6–8 weeks of age.

Related to this disagreement, Johnson and de Haan (2001) hypothesized that, in the first few weeks of life, face recognition is mediated by an early hippocampal-based pre-explicit memory (Nelson, 1995). This hippocampal-system is thought to form an accurate representation of the memory of the visual stimuli, independent of whether they are face-like or non-face-like. According to this hypothesis, newborns can discriminate between individual faces by memorizing the shape of their individual features (e.g., Simion, Farroni, Macchi Cassia, Turati, & Dalla Barba, 2002).

On the other hand, this type of face processing in infants is thought to differ from that in adults. de Haan, Johnson, Maurer, and Perrett (2001) suggested that once higher cortical areas begin to mediate, they would relate one memorized face to another. Through extensive experience with faces, this cortical area would enable infants to mentally form average prototypic representations of faces after 6–8 weeks. This leads the infants to encode new faces in terms of the way in which they deviate from the prototype; this allows them to discriminate between individual faces (Valentine, 1991).

Thus, the ability to form a prototypic representation of the face appears to develop only after 6–8 weeks, with the emergence of a functional cortical system for face processing. This view was supported by de Haan et al. (2001). They familiarized 1- and 3-month-olds to four individual faces, and tested whether they recognized a computer-generated image of a face comprised of the average of the four faces, and one of the exact individual faces. Recognition of the average face was tested by showing the baby a pair of faces consisting of: (1) the average and (2) one of the four faces seen during familiarization. Recognition of an individual face was tested by showing the baby a pair of faces consisting of: (1) an unfamiliar face and (2) one of the four faces seen during familiarization. The results showed that both 1- and 3- month-olds were able to recognize familiar individual faces. However, only the 3-month-olds looked longer at the familiar than the average face.

When and how do human infants discriminate between and recognize individual faces? Are there any developmental changes in processing faces? Comparative studies to determine the phylogenic origin of human face recognition will help reveal answers to these questions. Several studies have investigated whether non-human primates could discriminate between the faces of conspecific adults (e.g., pigtailed macaques, Lutz, Lockard, Gunderson, & Grant, 1998; Swartz, 1983; chimpanzees, Itakura & Matsuzawa, 1993; Tomonaga, Itakura, & Matsuzawa, 1993). However, only a few systematic reports have focused on the development of face recognition in non-human primates.

In this study, we observed our closest evolutionary relatives, the chimpanzees (*Pan troglodytes*). They have much in common with humans, especially during the early stages of life. Recent comparative experiments suggest the existence of similarities between the early social competence of human and chimpanzee neonates (e.g., social smiling, Bard, Platzman, Lester, & Suomi, 1992; Mizuno & Takeshita, 2002; facial imitation, Myowa, 1996; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004; detection of eye gaze direction, Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003). It is possible that humans and chimpanzees posses a shared ability to process faces.

The purpose of the current study was to systematically examine a single developmental change in face processing in infant chimpanzees, aged 1–18 weeks. Two experiments were conducted using preferential-looking procedures. In Experiment 1, we examined the chimpanzee's ability to discriminate the mother's face. In Experiment 2, we used the faces of other species (humans) as test stimuli. Several studies have suggested that once a prototype that is human face specific is formed, it becomes difficult for human adults to discriminate between individuals of other races in comparison to their own races (Chance, Turner, & Goldstein, 1982; Goldstein & Chance, 1980; Rhodes, Tan, Brake, & Taylor, 1989). We postulated that, before forming a prototype that was more "chimpanzee face specific," they would be able to memorize the most familiar face of the other species.

In addition, we also created computer-generated "*enhanced*" faces of their mothers and the familiar humans. The only difference between the *normal* and the *enhanced* faces were the relative positions of several feature points, which deviated from those of the prototype face. Given that the chimpanzees memorize the mother's face based on the shape of local information, it might be difficult for them to discriminate between the two faces. On the contrary, if they encode the individual faces based on the prototype, they might begin to detect the difference between the two faces.

2. Experiment 1

2.1. Method

2.1.1. Chimpanzees

Three infant chimpanzees, a male named Ayumu and two females named Cleo and Pal, participated in the experiment (Fig. 2). These infants had been reared since birth with their biological mothers at the Primate Research Institute of Kyoto University (Matsuzawa, 2003). During the daytime, they spent most of their time in an outdoor compound (approximately 700 m^2, Ochiai & Matsuzawa, 1998) with eight adult chimpanzees. At night, each mother–infant pair entered a separate bedroom and rested. The three infants had participated in a research project on chimpanzee development, and had therefore, experienced a variety of tests related to the development of cognitive abilities (Myowa-Yamakoshi et al., 2003; Myowa-Yamakoshi et al., 2004; Tomonaga et al., 2004). Their mothers had also participated in several cognitive experiments (Kawai & Matsuzawa, 2000; Matsuzawa, 1985, 2001; Myowa-Yamakoshi & Matsuzawa, 1999, 2000; Tanaka, 1996; Tomonaga, 1998). The care and use of the chimpanzees were in accordance with the 2nd version of the Guide for the Care and Use of Laboratory Primates (2002) of the Primate Research Institute, Kyoto University.

2.1.2. *Stimuli*

The stimuli consisted of three color pictures: (1) a "*normal*" face of the chimpanzee's mother, (2) an "*enhanced*" face of the chimpanzee's mother, and (3) an "*average*" face that was generated from that of eleven chimpanzees in the Primate Research Institute of Kyoto University (Fig. 1).

The photographs used in the experiment were taken with a digital camera (Olympus, model C-990 Zoom) and were processed using a software package (Software Morph). This software is based on the Facial Image Processing System (Yamada, Chiba, Tsuda, Maiya, & Harashima, 1992; Yamaguchi, Hirukawa, & Kanazawa, 1995) and consisted of two independent procedures for creating the *average* face. The first procedure involves averaging the form of a 3D wire-frame model. This 3D wire-frame model was composed of several 2D triangular areas. Using 38 feature points, the wire-frame model was transformed to fit each face by manually changing the fitting points. Using this model, we averaged the values of the 3D coordinates of each point. The second procedure involves averaging the brightness of the three colors (red, green, and blue) of each pixel. This procedure allowed the construction of the 2D patterns of the facial surfaces. For creating the *enhanced* face, we increased the difference for each corresponding point between the *average* and the target faces by 1.5 times. Further technical details are available in other studies (Brown and Perrett, 1993; Harashima, Aizawa, & Saito, 1989; Yamada et al., 1992; Yamaguchi et al., 1995).

These photographs were printed using a laser color printer (EPSON PM770); they were then enlarged to 18.0 cm × 15.0 cm and mounted on a poster board. The faces were cropped such that they occupied most of the photograph. This stimulus size was identical to those used by Myowa-Yamakoshi and Tomonaga (2001), to compare the results of the two species (gibbon and chimpanzee). The size appeared to be adequate for the two species to suitably view it from the testing distance of 30 cm (see Section 2.1.3).

2.1.3. *Procedure*

To assess the developmental changes in processing faces, the chimpanzees were tested twice every week between 1 and 18 weeks of age (Ayumu: 3–18 weeks except 13 and 17 weeks; Cleo: 4–17 weeks; Pal: 1–11 weeks).

The observation was conducted in a chimpanzee experimental booth (2.0 m × 2.0 m × 2.4 m). In the booth, a human tester sat face-to-face with an infant, who was held by his/her mother. The infant was shown one photograph. The tester positioned the stimulus directly in front of the infant's face at a distance of approximately 30 cm. As soon as the chimpanzee fixated the stimulus, it (the stimulus) was moved slowly to one side (right or left) at a rate

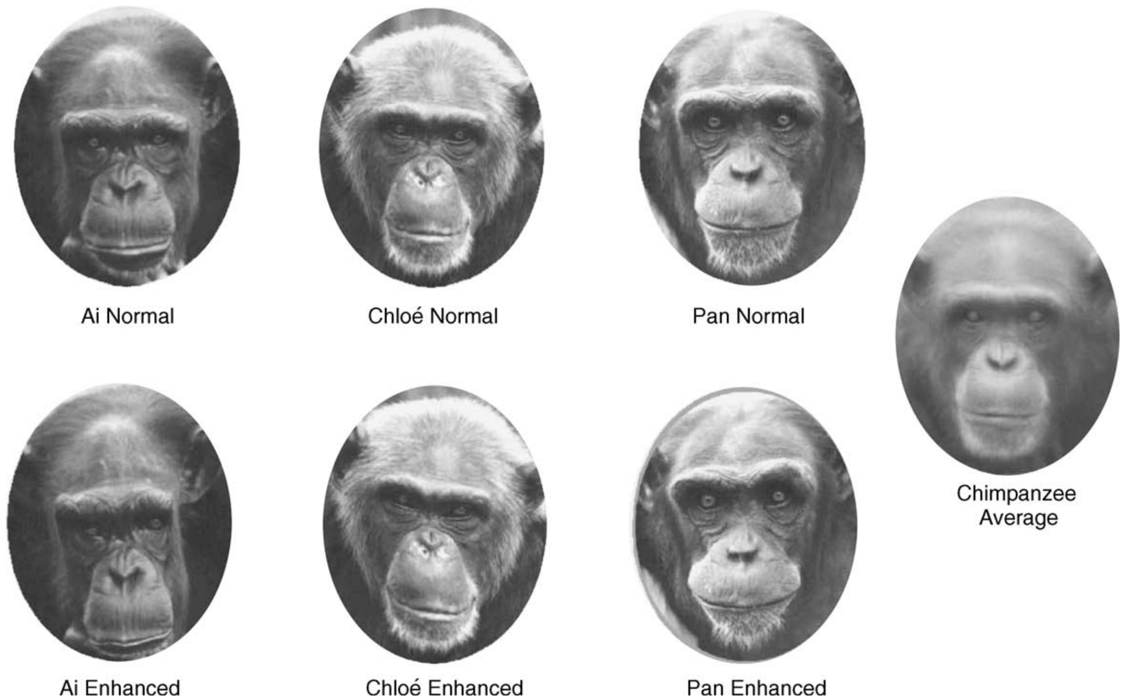

Fig. 1. The seven face photographs used in Experiment 1. Ai is the mother of Ayumu. Chloé and Pan are the mothers of Cleo and Pal, respectively.

Fig. 2. Experimental situation for Cleo. The infant, facing the human tester, was shown one face photograph. A small CCD camera was attached to the bottom part of the stimulus. The infant's reactions were recorded.

of approximately eighteen degrees per second. This procedure was defined as one trial and was repeated five times for each side (5 trials), regardless of whether the chimpanzee responded with a head or eye turn. Each session consisted of 10 trials (5 trials $\times$ 2 sides) for each stimulus. Thus, each chimpanzee participated in 60 trials (1 session $\times$ 3 stimuli $\times$ 2 days) per week. The infant's eye and head turning responses in pursuit of the stimulus were recorded on videotape for later analysis. We attached a small CCD camera (Sony, CCD-MC100) onto the bottom of the stimulus, so that the chimpanzee's tracking performance could be accurately recorded (Fig. 2). The order of presentation of each stimulus was randomly selected for each session.

2.1.4. Data analysis

The videotapes were coded to determine which face the infant looked at more. For each stimulus, the tracking response of each trial was assigned a score of either 1 or 0, depending on whether the chimpanzee fixated the stimulus with an eye or head turn of approximately more than 60 degrees (Myowa-Yamakoshi & Tomonaga, 2001). The maximum potential score for each stimulus per session was 10.

Two judges independently scored the chimpanzee's responses. To assess the reliability of the data, one judge checked all the trials. The other judge, who was blind both to the purpose of the study and to the stimulus that the infant was actually looking at, scored 10% of the trials (approximately 240 trials) for all the infants. The reliability between the two judges was sufficiently high (Cohen's κ. Ayumu: 0.91; Cleo: 0.74; Pal: 0.82).

2.2. Results

2.2.1. Developmental changes in tracking the faces

We calculated the mean tracking scores per week of age for each of the three facial conditions for each chimpanzee. Fig. 3 shows the developmental change as a mean percentage of the scores for each of the three facial conditions for each week of age tested. There was no considerable individual difference among the chimpanzees.

We found consistent developmental changes in the facial recognition ability of the three infants. Prior to 4 weeks of age (0 month), the infants showed few tracking responses and no differential responses to the three faces ($M = 34.2\%$). On the other hand, from 4 to 8 weeks of age (1 month), they showed a strong tracking for the mother's face ($M[normal] = 73.8\%$, $M[enhanced] = 70.0\%$, $M[average] = 26.7\%$). Moreover, after 8 weeks of age (2 months), they again showed no differences, but exhibited frequent tracking responses ($M = 76.5\%$).

A repeated two-way ANOVA was performed with month of age (1 month, 2 months) × stimulus (*normal*, *enhanced*, *average*). There was a main effect of stimuli, $F(2,4) = 7.51$, $p < 0.05$. The two-way interaction of age and stimulus was also significant, $F(2,4) = 13.98$, $p < 0.05$. Eye tracking at 1 month for the *average* face was significantly less than that at 2 months, $F(1,6) = 31.54$, $p < 0.01$. Moreover, at 1 month of age, there was a significant difference among the three faces, $F(2,8) = 33.52$, $p < 0.001$. Post-hoc multiple comparison tests (significance level defined by Ryan's procedure) revealed significant differences between the *normal* and the *average* faces ($p < 0.05$) and the *enhanced* and the *average* faces ($p < 0.05$) at 1 month of age.

Considered together, the infants began to perform more tracking for the *normal* and the *enhanced* mother's faces at 1 month of age in comparison to the *average* face. On the other hand, at 2 months of age, they again showed no differences but exhibited frequent tracking responses. In particular, the tracking responses for the *average* face increased dramatically during this period.

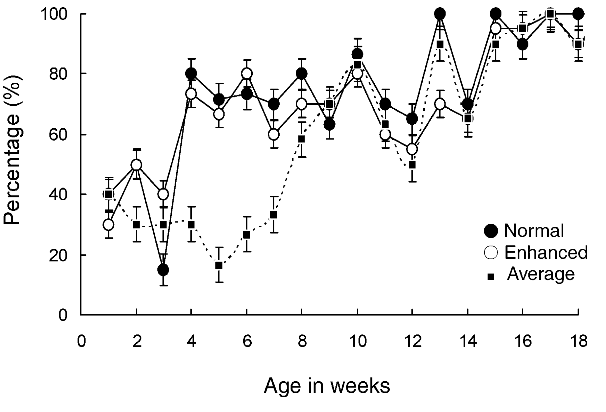

Fig. 3. Developmental change as a mean percentage of the tracking scores for each of the three conditions of the mother's face for each week of age (plus standard error).

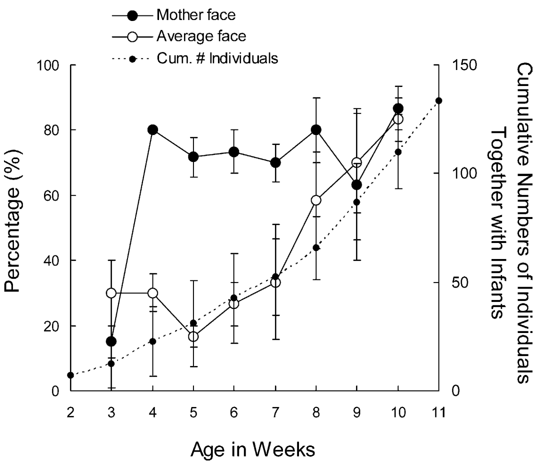

Fig. 4. The relationship between the mean percentage of the tracking scores for each of the two faces and the cumulative numbers of chimpanzee co-residents between 2 and 11 weeks (plus standard error).

2.2.2. *Factors influencing developmental change in face discrimination*

Since birth, we separated each mother–infant pair apart form other chimpanzees, because the mothers seemed to be very cautious about other chimpanzees who might peek at or touch their infants. As a result, during the first few weeks of life, each chimpanzee spent most of the time only with his/her mother in their bedrooms.

After this "isolation" period, we gradually started giving the infants and their mothers the opportunity to spend time with the other chimpanzees in the same enclosure for 30 min per day. We recorded the number of chimpanzees that each infant met in the compound on a daily basis. We thus calculated the cumulative numbers since birth for every week. Ayumu began to experience other chimpanzee faces from 2 weeks of age, Cleo from 4 weeks, and Pal from 1 week.

As discussed above, from 2 months of age, the infants performed frequent tracking responses, especially for the *average* face. We expected that the increasing visual experience of other chimpanzees could be a key factor in the developmental change in tracking the *average* face.

Fig. 4 shows the relationship between the mean percentage of the total tracking scores for each of the two faces and the cumulative numbers of chimpanzees that lived with the infants during weeks 2–11. Here, the data for the *enhanced* face was omitted because there was no difference between tracking responses for the *normal* and the *enhanced* faces. We calculated Pearson's correlation coefficients between the mean percentage of the total tracking scores for each of the two faces and the cumulative numbers (*normal*, $r = 0.52$, *average*, $r = 0.92$). The difference between these correlation coefficients approached significance ($t[5] = 2.47$, $p = 0.057$, Hotelling procedure). These results indicate that the developmental changes in tracking the *average* face appeared to correlate with the accumulation of visual experience of other chimpanzees' faces.

2.3. Discussion

The results show that the infant chimpanzees paid a greater amount of attention to their mother's faces, both the *normal* and the *enhanced*, in comparison to the *average* face, starting at 1 month of age. On the other hand, at around 2 months, all the presented faces equally elicited frequent tracking responses. This suggested that the *average* face also became attractive to the infants during this period.

In the first few weeks of life, human infants are believed to memorize the mother's faces on the basis of the shape of local elements (Simion et al., 2002). Subsequently, at around 6–8 weeks, they may begin to discriminate individual faces in relation to the prototypic representation of faces (de Haan et al., 2001; Johnson & de Haan, 2001; Nelson, 1995).

According to this view, our findings are subject to two interpretations. First, it was not until 4 weeks of age that the chimpanzees might have accurately memorized their mother's faces based on the shape of individual facial features. Second, at that time, the chimpanzees might have already formed a prototype of faces. If so, they might have discriminated the mother's faces based on this prototype.

Debating these interpretations, it is necessary to consider a difference in the amount of early visual experience of faces between humans and chimpanzees. It is noteworthy that the chimpanzees' face-to-face interactions with mothers and infants are much less than those of humans. Bard et al. (in press) observed the same mother–infant pairs during the infants' first 3 months of life and found that their mutual gaze occurred at a rate of 11.1–27.5 times an hour. It is reasonable to assume that compared with humans, the chimpanzees restricted experience of viewing would cause a lag in memorizing the mother's face at an individual level. We assume that at around 4 weeks of age, the chimpanzees began to recognize the mothers' faces by memorizing information such as the shape of the facial elements.

The same may be said about the process of forming a prototypic representation of faces in chimpanzees. Its emergence would also be later than that in humans. Generally, human newborns are frequently exposed to people other than their mothers from immediately after birth. On the other hand, until 0–3 weeks of age, the infant chimpanzees and their mothers were "isolated." Consequently, the infants had fewer opportunities to look at other chimpanzees' faces during this period. It is likely that, at around 8 weeks, when the *average* face also became attractive to the infants, they might begin to form an average prototypic representation due to extensive visual experience with other chimpanzees' faces.

With regard to this view, we hypothesized that once a prototype has been formed, it might become easier for the chimpanzees to discriminate between the *normal* and the *enhanced* faces. Prior to forming the prototype, it can be assumed that they discriminate between individual faces by an accurate representation in memory of their individual features. On the other hand, after forming a prototype, they might encode the individual faces in terms of the way in which they deviate from the prototype. However, our results did not support this hypothesis; no difference was observed between the tracking responses for the two faces of the mother throughout the testing period. A more detailed investigation into the developmental relationship between the two types of face processing in chimpanzees (i.e., an accurate representation in memory of an individual stimulus versus forming a prototype representation) is necessary.

The next experiment explored the same chimpanzees' ability to discriminate among individuals of another species (humans), for a direct comparison with the results for their own species. Several studies have suggested the difficulty for human adults to recognize unfamiliar individuals of other races compared to their own race (Chance et al., 1982; Goldstein & Chance, 1980; Rhodes et al., 1989). This can be explained by the view that human adults have already formed a "human face specific" prototype. We postulated that, prior to having formed a prototype that was more "chimpanzee face specific" (8 weeks), they would also be able to accurately memorize the most familiar face among other species, similar to that of their own (mother's face).

3. Experiment 2

3.1. Method

3.1.1. Chimpanzees

The chimpanzees were the same as those that participated in Experiment 1 and were observed from 1 to 18 weeks of age (Ayumu: 3–18 weeks except 13 and 17 weeks; Cleo: 4–17 weeks; Pal: 1–11 weeks).

3.1.2. Stimuli

The stimuli consisted of three color pictures: (1) a "*normal*" face of the most familiar human, (2) an "*enhanced*" face of the most familiar human, and (3) an "*average*" face created from pictures of Japanese humans (half were males and half were females). For Ayumu, the experimenter *Ma* was the most familiar human. Ayumu's mother, Ai, permitted only *Ma* to enter the same room as them. For the same reason, the experimenters *To* and *Ta* were the most familiar faces for Cleo and Pal, respectively. From their first week of life, they spent at least 2 h per day with their experimenter, performing various cognitive experiments (see Section 2.1.1). The mothers were not particularly unwilling to allow each familiar human visual access to their babies. With the exception of the three pairs, other humans were not allowed to enter the same booth as the chimpanzees.

The method for the *average* face was the same as that in Experiment 1. The photographs were enlarged to approximately 18.0 cm × 15.0 cm and mounted on a cardboard; the faces were cropped so that they occupied most of the photograph.

3.1.3. Procedure

The procedure was identical to that used in Experiment 1.

3.1.4. Data analysis

The data were analyzed in the same manner as in Experiment 1. Reliability between the two judges was sufficiently high (Cohen's κ. Ayumu: 0.87; Cleo: 0.82; Pal: 0.92).

3.2. Results

3.2.1. Developmental changes in tracking the faces

Fig. 5 shows the developmental change as a mean percentage of the total scores for each of the three facial conditions for each week of age tested. There was no considerable individual difference among the chimpanzees.

A repeated two-way ANOVA was performed with month of age (1 month, 2 months) $\times$ stimulus (*normal*, *enhanced*, *average*). The analysis provided no significant main effects or interactions.

3.3. Discussion

In contrast to the results of Experiment 1, we did not find clear evidence indicating the ability to discriminate between the human faces during the testing period. This can be interpreted as follows.

Nelson (1995) proposed that the ability to recognize faces developmentally "narrows" with extensive experience in processing the most frequently observed faces. As a result, by adulthood, human faces can be represented as a "human face specific" prototype. This hypothesis is supported by Pascalis, de Haan, and Nelson (2002). They demonstrated that 6-month-olds, but not 9-month-olds and adults, could discriminate between another species' (monkey) faces. On the contrary, adults are worse at recognizing unfamiliar individuals of other races compared to their own race (e.g., Goldstein & Chance, 1980).

As with the results of Experiment 1, we assumed that, at around 2 months of age, the chimpanzees would begin to form a face prototype formed from frequently seen faces. If the prototype is more "chimpanzee face specific," discriminating between another species' (human) faces would be more difficult. However, even before the infants formed a face

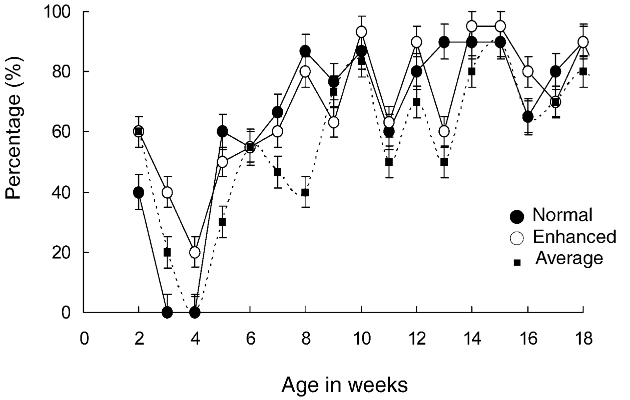

Fig. 5. Developmental change as a mean percentage of the tracking scores for each of the three conditions of the most familiar human's face for each week of age (plus standard error).

prototype, they showed no evidence of memorizing particular human faces. One explanation for the results may be that, at 18 weeks of age, the chimpanzees did not have enough experience with even the faces of the most familiar humans to memorize them as accurately as they had memorized their mothers' face. There is also the possibility that we stopped this experiment too early to find any evidence of recognizing the human faces.

4. General discussion

Two experiments examined the ability of 1–18-week-old infant chimpanzees to recognize the faces of the mother and highly familiar humans. We demonstrated that the infant chimpanzees were able to recognize the mother's face at around 1 month of age. By 2 months, they seemed to form a prototypic representation due to the extensive experience with other chimpanzees' faces. According to the Johnson and Morton's (1991) theory, we can interpret these results as follows; while CONSPEC served to orient the chimpanzees to faces, the hippocampal-system enables them to memorize the most attractive face (generally the mothers' faces), not relating one face stimulus with another. By 6–8 weeks of age, when the cortical systems (CONLERN) might become influential, the chimpanzees could form the prototypic representation due to the extensive experience with other chimpanzees' faces. Based on the cortical systems, they might begin to recognize individual faces.

However, the infant chimpanzees did not show evidence of recognizing the human faces throughout the testing period. There are several ways to explain the reason for this. However, for the moment, we can extend the argument to the idea of the influences of rearing environments on the development of face processing. The studied chimpanzees had a lot of experience with human faces since their birth. If the face processing system develops flexibly depending upon extended exposure to faces, it is possible that they form a prototype representation based on "mixed" information from human and chimpanzee faces.

There are only two studies with direct relevance to this point. Myowa-Yamakoshi and Tomonaga (2001) tested a "nursery-reared" infant lesser ape, the gibbon (*Hylobates agilis*). This gibbon was raised by human caretakers from 2 weeks of age. By 4 weeks of age, when the experiment started, he was observed to already prefer looking at a familiar caretaker's face to an unfamiliar human's face. It is noteworthy that the gibbon preferred the unfamiliar "human" face to an unfamiliar "gibbon" face.

The other is a study by Yamaguchi, Kanazawa, Tomonaga, and Murai (2003). They examined Japanese monkeys (*Macaca fuscata*) reared by human caretakers. The monkeys showed preferences for human faces, both averaged, and their caretaker's, after 3 h of visual experience with human faces. These findings suggest that non-human primates reared in a human environment might form a more "human face specific" prototype than their own species face prototype because of their daily interactions with humans.

The ability of face processing may develop flexibly, depending upon extended exposure to the surrounding faces immediately after birth. Further developmental and comparative studies will help to reveal the relationship between species-specific biological foundation and the effect of the postnatal visual experience in the development of face processing.

Acknowledgements

We thank N. Nakashima, A. Ueno, Y. Mizuno, S. Okamoto, T. Imura, C. Douke, M. Hayashi, K. Kumazaki, N. Maeda, A. Kato, K. Matsubayashi, G. Hatano, and O. Takenaka for help throughout this project. Supported by Grants-in-Aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology (MEXT), Japan (grant #12002009 and # 16002001 to T. Matsuzawa, #13610086 to M. Tomonaga, #09207105 to G. Hatano, #10CE2005 to O. Takenaka), the MEXT Grant-in-Aid for the 21st Century COE program A2 to Kyoto University, the Cooperative Research Program of the Primate Research Institute, Kyoto University to M.K. Yamaguchi, and the Research Fellowship #3642 to M. Myowa-Yamakoshi from the Japan Society for the Promotion of Science (JSPS) for Young Scientists. We gratefully acknowledge K.A. Bard, J.R. Anderson, and G. Yamakoshi for their helpful comments on an earlier draft of this article.

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