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Is attentional prioritisation of infant faces is unique in humans?: comparative demonstrations by modified dot-probe task in monkeys

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ABSTRACT
Humans innately perceive infantile features as cute. The ethologist Konrad Lorenz proposed that the infantile features of mammals and birds, known as the baby schema (kindchenschema), motivate caretaking behaviour. As biologically relevant stimuli, newborns are likely to be processed specially in terms of visual attention, perception, and cognition. Recent demonstrations on human participants have shown visual attentional prioritisation to newborn faces (i.e., newborn faces capture visual attention). Although characteristics equivalent to
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those found in the faces of human infants are found in nonhuman primates, attentional capture by newborn faces has not been tested in nonhuman primates. We examined whether conspecific newborn faces captured the visual attention of two Japanese monkeys using a target-detection task based on dot-probe tasks commonly used in human visual attention studies. Although visual cues enhanced target detection in subject monkeys, our results, unlike those for humans, showed no evidence of an attentional prioritisation for newborn faces by monkeys. Our demonstrations showed the validity of dot-probe task for visual attention studies in monkeys and propose a novel approach to bridge the gap between human social cognition research and primate research. This suggests that attentional capture by newborn faces is not common to macaques, but it is unclear if experiences of caretaking influence their perception and recognition of infantile appraisal stimuli. We need additional comparative studies to reveal the evolutionary origins of baby-schema perception and recognition.

1. Introduction

Humans innately perceive infantile features as cute (Alley 1981, 1983; Fullard and Reiling 1976; Sanefuji, Ohgami, and Hashiya 2007; Sprengelmeyer et al. 2009). The ethologist Konrad Lorenz proposed that infantile features, known as baby schema (kindchenschema), motivate caretaking behaviour and act as a “social releaser” (Lorenz 1943). He defined baby schema as a set of infantile physical characteristics; these include a round face, large head, large
eyes, a high and protruding forehead, chubby cheeks, a small nose and mouth, short and thick extremities, and a plump body shape. Lorenz’s theory held that the evolution of this adult perception or social cognition was shaped by the selective advantages of the survival of immature offspring. Several empirical psychological (Alley 1981, 1983; Brosch et al. 2008; Brosch, Sander, and Scherer 2007; Fullard and Reiling 1976; Glocker, Langleben, Lobmaier et al. 2010, Ruparel, Loughead, Gur et al. 2009; Hodsoll, Quinn, and Hodsoll 2010; Luo, Lee, and Li 2011; Parsons et al. 2011; Sanefuji, Ohgami, and Hashiya 2007), endocrinological (Sprengelmeyer et al. 2009), and neuroimaging (Glocker, Langleben, Ruparel, Loughead, Valdez et al. 2009) studies have supported his ideas. However, all such studies have been conducted in humans. As infantile physical features are present in other mammalian and avian species, it is surprising that research of this sort has been conducted in nonhuman animals only rarely.

The operation of specialised visual processing underlying perception of and visual attention devoted to newborn faces has been recently reported in humans (Brosch et al. 2008; Brosch, Sander, and Scherer 2007; Hodsoll, Quinn, and Hodsoll 2010; Parsons et al. 2011). It is well known that threat-relevant stimuli, such as angry faces or snakes, automatically evoke an emotional response, likely resulting in the capture of visual attention in humans (LoBue and DeLoache 2008; Öhman 2005; Öhman, Flykt, and Esteves 2001). This suggests that the human brain implements a fear module when the amygdala rapidly detects threat-relevant stimuli such as a fearful face or snake.
However, appraisal theories of emotion hypothesise that the human brain is specialised for processing not only threat-relevant but also biologically relevant stimuli (e.g. Scherer 2001). In terms of survival, there is no doubt that newborns are typical examples of biological relevant stimuli with ecological validity. Recently reports of attentional capture by newborn faces in humans suggest that human attentional systems prioritise newborn faces as well as images of snakes (Brosch et al. 2008; Brosch, Sander, and Scherer 2007; Lobmaier et al. 2010; Parsons et al. 2011).

Given considerations of biological relevance, it is plausible that attentional prioritisation would be not restricted to humans. Indeed, in the context of the common foundations for neural processing and the similar social systems shared by human and nonhuman animals (Adolphs 1999), it would be unsurprising to find that what is biologically relevant for humans would also be relevant for nonhuman primates. For example, an equivalent attentional capture by snake stimuli has recently been reported in Japanese macaques (Shibasaki and Kawai 2009). Consistent with Lorenz’s predictions and similar to findings in humans, attentional capture by newborn faces may also be observed in monkeys.

To examine the evolutionary continuity of the human attentional prioritisation of baby schema, we compared the visual attention paid by two female Japanese macaques (Macaca fuscata; JM) to images of newborn faces with that paid to adult faces using a target-detection task based on the dot-probe
task commonly used in human visual attention studies (Brosch et al. 2008; Brosch, Sander, and Scherer 2007; Hodsoll, Quinn, and Hodsoll 2010). The dot-probe task is a well-established paradigm for investigating attentional prioritisation in humans. This task requires participants to detect a small dot-probe target as quickly as possible. The dot-probe target is shown separately on the left and right sides of the screen, and the visual cueing consists of two paired stimuli that are presented briefly before the target appears. When either of the two stimuli captures most of the participant’s attention, the target-detection time is decreased. To employ this dot-probe task with monkeys, we used a touch-sensitive screen monitor and conditioned monkeys to touch the target key to signal detection. We determined whether cueing by infant faces influences the time to target detection.

2. Materials and methods

All procedures complied with the Guide for the Care and Use of Laboratory Primates (Third Edition, the Primate Research Institute, Kyoto University, 2010) and were approved by the Ethics Committee of the Primate Research Institute of Kyoto University (#2012-065).

2.1. Subject animals

Two 5-year-old female Japanese macaques (T2152, A2194) participated in the experiments. Both were born in different social groups at the Primate Research Institute of Kyoto University (Japan) and lived with their own mother.
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and other group members. Their original groups were equivalent social structures with wild ones, including several adult males and females and subadult daughters and sons. Both subjects lived in those groups. T2152 was moved to group cages when she was 20 months old, and lived with 5-6 same age peers until 5 years old. A2194 was moved to group cages when she was 14 months old, and lived at group cage until 4 years old. After living in group cages, they moved to individual cages, allowing them to visually and vocally interact with other monkeys, but separated from their own group members. They were fed daily with monkey pellets and fruits, and received water freely. A captive Japanese macaque is sexually matured around between 4 and 5 years old, therefore they were sexually matured during our experiments, but were nulliparous with no experience of mating.

2.2. Apparatus

The experimental tasks were performed in a custom-made experimental operant box (450 mm W × 450 mm D × 600 mm H) in a sound-attenuating chamber. The monkeys were individually tested in the box. A 15-inch touch-sensitive LCD screen (TSD-CT157-MN, Mitsubishi Electric Engineering, Tokyo, Japan, 1024 × 768 pixels display resolution) was mounted on one side of the experimental box. A universal food dispenser (BUF-310-P100, BIOMEDICA, Osaka, Japan) was placed in the experimental box to provide a piece of sweet potato or raisins as a food reward. The food dispenser was controlled by computers with USB I/O interfaces (DIO-0808TY-USB, CONTEC, Tokyo, Japan). Stimulus presentation and food dispensing were controlled by a
2.3. Stimuli

Images of the faces of conspecifics were used as visual cues, and we prepared two stimulus categories: adult females (sexually mature, ≥4 years old) and infant females (<1 year old). All faces, which were unfamiliar to subjects, were oriented frontward, displayed no emotion, and appeared on a uniform black background. All images fit within an area of 300 × 300 square pixels. The average luminance and contrast were adjusted to equivalent values using Adobe Photoshop CS5. Five stimuli were prepared for each of the two stimulus categories (see Fig. 1).

2.4. Procedures

Monkeys were required to touch the circle keys on the screen throughout the experiments. At the start of each trial in the training session, one white circle was presented at the centre of the screen as a start key. When the start key was touched, the screen immediately blacked out for 100 ms. After the blackout, a blue circle was displayed on either the left or the right side of the screen as a target key. When a target key was touched, the screen blacked out and the monkey was reinforced with a food reward accompanied by auditory feedback. After reinforcement, a 2000-ms inter-trial-interval (ITI) was inserted, and next trial then started. The monkeys were required to touch the target key within 1000 ms. When the monkey did not touch within 1000 ms, the screen blacked out and a buzzer sound was played. After the time out, a 10000-ms ITI was
inserted as negative feedback, and the next trial then started. A single training
session consisted of 100 trials (50 for the left target, 50 for the right target
presented in a randomised order). When >80 % correct responses were
recorded in five consecutive sessions, the participants were considered to have
learned how to perform the tasks. These five consecutive sessions were used
to provide baseline data regarding target detection without visual cues.

After the baseline sessions, we proceeded to the cued session (Fig. 2).
After the start key was touched, a cue was presented for 100 ms. The cue
consisted of one infant and one adult face. The paired stimuli were randomly
selected from five infant and five adult faces. Following cue presentation, the
target key appeared. In infant-valid trials, the target key appeared near the
infant’s face; in adult-valid trials, the target key appeared near the adult’s face
(Fig. 1). Half of the trials in each session were infant valid, and the other half
were adult valid. Both side-by-side positions (left infant and right adult, left adult
and right infant) were used, yielding a total of 100 trials per a session (five
infants x five adults x two side-by-side positions x two validity conditions).
Presentation orders were randomised. Ten test sessions were conducted with
each subject.

2.5. Analysis
We measured the reaction times (RTs) from the appearance of the response
key to the touch response. Trials that timed out were excluded from the analysis
of RTs. RTs for experimental conditions were averaged for each session. First,
to examine the effect of cue presentation, we compared the RTs during the five baseline sessions with those during the 10 test sessions with a two-way repeated-measures analysis of variance (ANOVA); we tested for main and interaction effects involving cue presentation (baseline, test) and target position (left, right). Second, to examine the effects of the cue-validity condition (infant valid, adult valid) and target position (left, right) on RTs, we compared RTs under the infant- and adult-valid conditions with a two-way repeated-measures ANOVA; we tested for main and interaction effects involving cue validity and target position. Sessions were treated as error terms in all ANOVAs. The statistical analyses were performed separately for the two subjects. Significance levels were set at $P < 0.05$.

3. Results

Figure 3 shows the RTs during baseline and cued sessions for each target position (left or right) for the two monkeys. The ANOVAs showed no interaction effects between cue presentation and target position (T2152: $F_{1,13} = 3.68, P = 0.08$; A2194: $F_{1,13} = 1.86, P = 0.20$) but did reveal significant main effects for cue presentation in both subjects (T2152: $F_{1,13} = 6.82, P = 0.022$; A2194: $F_{1,13} = 6.61, P = 0.023$). A significant effect of target position was also observed in A2194 ($F_{1,13} = 37.3, P < 0.001$) but not in T2152 ($F_{1,13} = 1.32, P = 0.27$). This indicated that the subjects detected targets more rapidly when cues were presented than when they were not.
Figure 4 shows the RTs for both subjects under the infant- and adult-validity conditions for each target position (left or right) during the cued sessions. The ANOVAs revealed no interactions between cue validity and target position (T2152: $F_{1,27} = 0.87$, $P = 0.36$; A2194: $F_{1,27} = 0.072$, $P = 0.79$) but did reveal significant main effects for target position in A2194 ($F_{1,27} = 85.14$, $P < 0.001$) but not T2152 ($F_{1,27} = 0.037$, $P = 0.85$). We found no significant effect for cue validity in either subject (T2152: $F_{1,27} = 0.19$, $P = 0.66$; A2194: $F_{1,27} = 3.16$, $P = 0.089$). These findings indicate that target detection was not influenced by type of cue.

4. Discussion

Our data showed that two well-trained monkeys touched the target more rapidly with visual cues than without such cues. This suggests that the visual attention of monkeys was attracted by the visual cues. However, in contrast with the results of the recent study on humans, RTs were not influenced by the type of visual cue. The side bias of target position was found only in A2194, indicating that she always touched targets shown in left side of screens. It might be interesting because the previous studies using dot-probe task in humans reported a similar side bias and concluded that it would be caused by laterality in emotional processing. However, side bias found in A2194 would be caused not by laterality in emotional processing but rather by her handedness. She always touched screen by left hand. Those suggest that the monkeys’ attention was not captured by infant faces.
So far, two major experimental paradigms have been used for behavioural studies in human visual attention. One paradigm is dot-probe tasks which we used here, and the other is visual search task, which requires participants to simply detect a target visual stimulus among a lot of distracter stimuli on the screen as quickly and correctly as possible. If a target stimulus captures the visual attention than distracters, the detection time for visual search would be shortened. Although visual search paradigm has an advantage for simple discussions between participant performance and attentional prioritisation, it would be more difficult for monkeys and other animals to train those tasks. Animals must learn to discriminate a target stimulus from other distracters before testing attentional prioritisations. In dot-probe task, animals only learn to touch a small dot-probe target on the screen as quickly as possible without any discrimination learning. Despite of small sample size, our results confirming the validation of the paradigm would contribute to further comparable experiments in monkeys. For the next step, we need to know how the cue duration influences their visual attention. Here, we used single due duration (100 msec), because one of our purposes was to show comparative results with the previous studies (Brosch, Sander, and Scherer 2007) which used only 100-msec as cue duration. Usually, several cue durations from 100 to 500 msec have been used in dot-probe tasks in human participants. Influence of cue validity on target detection would varies according to cue durations. Longer cue duration might show attentional prioritisation to infant face in monkeys as well. To establish this paradigm more effectively, we will need to know their basic profiles of visual attentions during this paradigm.
Although attentional prioritisation was not found in monkeys, this does not rule out the possibility that monkeys have a cognitive process specialised for infant stimuli. Recently, using visual paired-comparison tasks, we found a visual preference for infantile features in nonhuman primates that was equivalent to the human preference for baby schema (Sato et al. 2012). We found that monkeys looked at images of infant bodies longer than they looked at those of adult ones and concluded that monkeys preferred images of infants over those of adults. This preference for babies in monkeys would be equivalent to that in humans (Alley 1981, 1983; Glocker, Langleben, Ruparel, Loughead, Gur et al. 2009; Glocker, Langleben, Ruparel, Loughead, Valdez et al. 2009; Luo, Lee, and Li 2011; Sanefuji, Ohgami, and Hashiya 2007) and could be explained from an ecological perspective in terms of the prolonged period of infancy that is characteristic of both species. Indeed, monkeys are also born immature and need adult nurturing. However, the psychological process of visual attention differs from that of visual preference. Because preferences for baby schema occur independently of attentional processes, we can conclude that monkeys possess a specialised preference for infants without also demonstrating that they place attentional priority on infants. Preference for infants may constitute a psychological trait that is common to humans and monkeys, whereas attentional prioritisation of infants might be unique to humans.

Brosch hypothesised that the attentional prioritisation of human baby schema may involve the amygdala as a possible candidate neural substrate.
(Brosch et al. 2008; Brosch, Sander, and Scherer 2007). Indeed, although numerous studies have confirmed the important role of the amygdala in neural processing involving the prioritisation of biologically relevant stimuli, most previous findings have related to threat-relevant stimuli such as snakes and angry faces rather than to emotionally positive stimuli such as smiling faces (for a review, see Öhman 2005). The perception and recognition of negative affectively arousing stimuli by both humans and monkeys likely involves the amygdala. However, the attentional prioritisation of baby schema seems to be an exceptional phenomenon found only in humans, who may have evolved special processing operations that prioritise attention to baby schema in a unique way. In fact, research conducted after Brosch’s studies has shown that the attentional prioritisation of baby’s faces does not hold for infants of another race (Hodsoll, Quinn, and Hodsoll 2010). Indeed, the attentional prioritisation of baby schema is restricted to babies of one’s own race, suggesting that it is not as generalised as are reactions to threat-relevant stimuli. These specialised perceptual traits do not derive from the common ancestor of humans and macaques.

In contrast to visual attention, cognitive process involved in visual preference would be partly shared by different species. For example, general preference for faces over non-face objects would be shared by nonhuman primates (Sugita 2008) and by avian species (Rosa-Salva et al. 2010; 2011) as well, suggesting common cognitive traits between humans and animals. Likely, visual preferences for baby schema may be underpinned by the neural substrates that
are common to humans and animals. A recent neuroimaging study in humans showed that baby schema activate the nucleus accumbens, a key structure in the mesocorticolimbic system mediating reward processing and appetitive motivation, as a function of degrees of cuteness (Glocker, Langleben, Ruparel, Loughead, Valdez et al. 2009). Interestingly, baby-schema activation was confirmed in nulliparous women, and it was suggested that brain-reward systems are likely involved in the perceptions of cuteness related to baby schema. This is thought to result in the promotion of human caregiving, irrespective of kinship relationship. Although no empirical evidence of the activation of the nucleus accumbens by baby schema has been reported in monkeys thus far, studies in rats have revealed that the nucleus accumbens plays an important role in maternal behaviour (Champagne et al. 2004). Many behavioural studies of monkeys have suggested that infants, regardless of their fitness, induce caregiving behaviour. Indeed, conspecific and heterospecific adoption of infants has often been observed in nonhuman primates (Thierry and Anderson 1986), and adoption in animals remains completely unexplained in terms of fitness considerations. It seems plausible that a baby would itself automatically provoke the motivation for caregiving. In the context of the recent evidence in monkeys (Sato et al. 2012), it seems plausible that the preference for babies evolved from the common ancestor of humans and macaques.

In conclusion, our results did not reveal the operation of any special attentional prioritisation for baby schema in monkeys; this contrasts with the results for humans. However, it is too early to conclude that monkeys do not place any
kind of attentional prioritisation on infant faces. We must acknowledge several limitations of our present research. First, we tested only two nulliparous females with no experience of caregiving. We should not conclude all from our restricted subjects. In the near future, we must test if exposures to babies or experiences of delivery influence the attentional prioritisation to infant stimuli like humans.

Second, context of face stimuli would influence cue validity. Given that attentional prioritisation was found in response to fear-relevant stimuli such as snakes or angry faces, the results may differ if we contextualise the face stimuli. For example, a facial image of an infant screaming may capture monkeys’ attention more strongly than a facial image of an adult screaming. It is also possible that infant faces specifically capture the attention of their own mothers.

In fact, a recent demonstration in humans revealed that the onset latency of event-related potentials (P300) was shortest when mothers observed their own infant crying, suggesting that the context of an infant face influences attentional prioritisation (Doi and Shinohara 2012). Future research with monkeys should consider the context of stimulus faces. Although why humans evolved this attentional prioritisation remains unclear, it may be related to the prolonged immaturity of newborn humans. There is no doubt that human babies are the least mature among the baby animals. Indeed, during the first years of life, human babies cannot survive without parental care. Attentional prioritisation may have evolved as a survival strategy to counter this immaturity. We need to conduct additional comparative studies to reveal the evolutionary origins of baby-schema perception and recognition.
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References


FIGURE LEGENDS

Figure 1. Stimuli used in experiments. (Top) Adult faces. (Bottom) Infant faces.

Figure 2. Schematic representation of the target-detection tasks for (A) baseline sessions, and (B) cued sessions. A trial under the right-target condition was conducted in the baseline session, and trials under the infant-valid and adult-valid conditions with the target on the left were conducted in the cued sessions.

On the screen, the circles for the start and target keys were both set at
153 pixels in diameter, and the horizontal distance between the left and right key positions (from centre to centre) was set at 724 pixels. The horizontal distance between paired stimuli was also adjusted to correspond to that between the response keys.

Figure 3. Reaction times (RTs) for cue-presentation and target-position conditions for T2152 (top) and A2194 (bottom). Error bars represent mean values ± 95% confidence intervals.

Figure 4. Reaction times (RTs) under the validity and target-position conditions for T2152 (top) and A2194 (bottom).
(A) Baseline session
- Start key
- No cue (100 msec)
- Target key
  Reaction required within 1000 msec
- Inter-trial Interval (ITI)
  2000 or 10000 msec

(B) Cued session
- Start key
- Cue (100 msec)
  Infant valid
- Target key
  Reaction required within 1000 msec
- ITI
  2000 or 10000 msec

- or -
- Cue (100 msec)
  Adult valid