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ORIGINAL ARTICLE

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An infant chimpanzee (*Pan troglodytes*) follows human gaze

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Abstract The ability of non-human primates to follow the gaze of other individuals has recently received much attention in comparative cognition. The aim of the present study was to investigate the emergence of this ability in a chimpanzee infant. The infant was trained to look at one of two objects, which an experimenter indicated by one of four different cue conditions: (1) tapping on the target object with a finger; (2) pointing to the target object with a finger; (3) gazing at the target object with head orientation; or (4) glancing at the target object without head orientation. The subject was given food rewards independently of its responses under the first three conditions, so that its responses to the objects were not influenced by the rewards. The glancing condition was tested occasionally, without any reinforcement. By the age of 13 months, the subject showed reliable following responses to the object that was indicated by the various cues, including glancing alone. Furthermore, additional tests clearly showed that the subject's performance was controlled by the "social" properties of the experimenter-given cues but not by the non-social, local-enhancing peripheral properties.

Keywords Chimpanzee · Infant · Gaze following · Joint attention · Social cues

Introduction

The ability to follow another individual's gaze has been demonstrated in young human infants. This ability is a required prerequisite for "joint visual attention". Scaife and Bruner (1975) demonstrated that human infants as young as 2 months adjust their gaze contingent on a change in the focus of attention of an adult, suggesting that 2-month-old infants are already sensitive to the gaze of others.

Butterworth and his colleagues (Butterworth and Cochran 1980; Butterworth and Jarrett 1991) conducted a series of experiments that replicated and extended these findings. They obtained evidence for three successive mechanisms of joint visual attention in infants ranging in age from 6 to 18 months. At 6 months, infants progress gradually from responding to the head movements of others to orienting in the same general direction within their visual field. By 12 months, infants are able to localize the particular object at which the other is looking. By 18 months, infants can follow someone else's gaze into space that is outside their own visual field (see Butterworth and Jarrett 1991).

This ability to follow the gaze of others is found not only in humans but also in some non-human animals, especially in primates. A variety of primate species visually track the gaze direction of conspecifics to external objects (chimpanzees, mangabeys, and macaques; Emery et al. 1997; Tomasello et al. 1998; Tomonaga 1999). Following the gaze direction of *conspecifics* is an important ability for social primates because it allows individuals to take advantage of the visual experience of group mates that spot interesting or important objects and events, such as food, predators, or significant social interactions. Furthermore, chimpanzees also visually follow the gaze direction of *humans*. They do this on the basis of eye direction alone, independent of head direction (Povinelli and Eddy 1996; Itakura and Tanaka 1998), even when the target is located above and/or behind them (Itakura 1996; Povinelli and Eddy 1997; Call et al. 1998).

Various related experiments have been conducted in other non-human primates. Peignot and Anderson (1999) tested captive lowland gorillas (*Gorilla gorilla*) on object-choice tasks in which the correct object was indicated by the human experimenter. They reported that the gorillas did not use the experimenter's gaze without head orientation. Anderson and Mitchell (1999) compared the propensity of lemurs (*Eulemur macaco*) and macaques (*Macaca*

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arctoides) to engage in visual co-orientation, defined as turning to look in the same direction as the human experimenter whose focus of attention changes. They reported that the macaques consistently showed visual co-orientation whereas the lemurs showed no such response. Itakura and Anderson (1996) demonstrated that a male capuchin monkey could learn to follow the experimenter's gaze in object-choice tasks after intensive training. He learned to use the following experimenter-given cues: tapping, pointing, and gazing plus head orienting, but he failed to use eye gaze cues alone to solve the task. However, Vick and Anderson (2000) found that the capuchin monkeys were able to learn to use the experimenter's glancing at the correct object as a cue.

Human infants progressively develop the ability for gaze following between 6 and 18 months of age, as described above. Although there is a huge amount of human infant literature, there are very few studies on joint visual attention/gaze following by young non-human animals. Myowa-Yamakoshi and Tomonaga (2001) found that at between 1 and 6 weeks of age, an infant gibbon (*Hylobates agilis*) preferred to look at a schematic direct-gaze face rather than an averted-gaze face, suggesting the possibility that non-human primates can discriminate gaze directions in very early infancy. Tomonaga et al. (2000) preliminarily reported that human-raised Japanese macaque infants (4–6 months of age) followed pointing and head-orienting cues made by the caregiver. Ferrari et al. (2000) assessed in juvenile and adult pig-tailed macaques (*M. nemestrina*) the ability to follow the eye gaze of an experimenter. The juvenile monkeys were not able to orient their attention on the basis of eye cues alone. Tomasello et al. (2001) studied the ontogeny of gaze following in two species: rhesus macaques and chimpanzees. The rhesus infants first began reliably to follow the direction of gaze at the end of the early infancy period, at about 5.5 months of age. Chimpanzees did not reliably follow human gaze until 3–4 years; this age corresponds to the latter part of the late infancy period for this species.

The present longitudinal study was conducted to clarify the ability in chimpanzees to follow experimenter-given cues – including tapping, pointing, gazing with head orientation, and glancing (eye movement alone) – in early infancy. Our study started at the neonatal stage (6 months of age) and ended in early infancy (17 months of age).

Experiment 1

We first presented a gaze-following task to a chimpanzee infant and observed longitudinally the developmental changes in response to the social cues, including gaze.

Methods

Subject

One male chimpanzee infant, Ayumu, served as the subject from 6 months to 13 months of age (see Fig. 1). Ayumu had been reared with his mother since birth at the Primate Research Institute, Kyoto University. Both lived in a community of 14 chimpanzees. Ayumu was born after artificial insemination of his mother. He is one of three subjects in a research project on chimpanzee development. He has experience with a variety of tests for the development of cognitive abilities (Holden 2001; Matsuzawa 2001a, b). He maintained his free-feeding body weight throughout the present study, that is, no food deprivation

Fig. 1 **a** The subject Ayumu, performing the experimental task. His mother worked at her own tasks in the same experimental booth. **b** Ayumu looked at the target object at which the experimenter pointed (reprinted with permission from *The Mainichi Newspaper*, Japan)

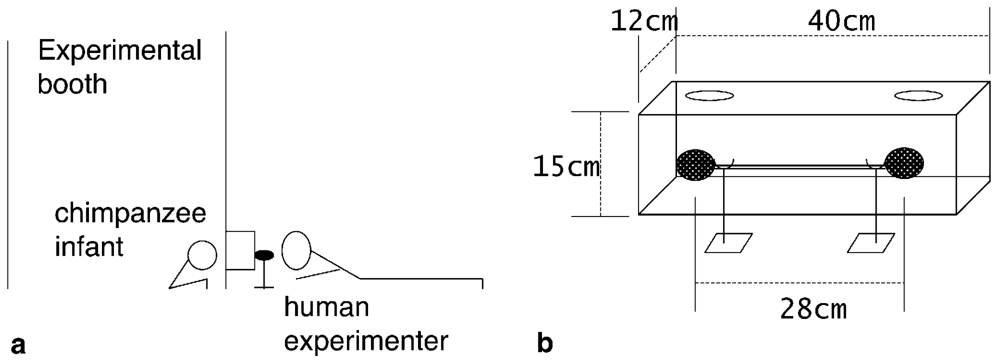

Fig. 2 **a** Experimental setting. **b** Schematic representation of the food tray and a pair of objects

was used. Care and use of the chimpanzee adhered to the *Guide for the care and use of laboratory primates* of the Primate Research Institute (1986).

Apparatus and stimuli

The experiment was conducted in the chimpanzee experimental booth at the Institute (Fig. 2a). The experimental apparatus consisted of a food tray (Fig. 2b) and objects that served as targets. The food tray (12×15×40 cm) was made of transparent acrylic board and was placed at the bottom of a wall in the experimental booth. Three small holes (4 cm) through which food rewards were given were on the top of the tray (14 cm apart center to center). At each trial, two identical toys (mean size 2 cm) were presented, each attached to one end of an acrylic bar (length: 28 cm). Forty-five different objects (such as golden balls, little teddy bears, little colored bells, etc.) were presented across the trials to keep Ayumu interested. The behavior of the chimpanzee was video recorded.

Prior to the experiment, Ayumu had been taken into this experimental booth with his mother five times per week since he was 11 days old. Thus, at the beginning of the experiment he was already very familiar with both the experimental booth and the experimenters.

Procedure

Ayumu came to the experimental booth with his mother. After his mother began working on another task [one of the visual discrimination tasks that had her facing a computer system (Kawai and Matsuzawa 2000; see Fig. 1a) at one side of the booth], the experiment for the chimpanzee infant began. At the onset of each trial, the experimenter laid on the floor outside the booth, 20 cm behind the objects (see Fig. 2a). She called the subject by name or made a play face to attract his attention. After Ayumu approached the food tray, the experimenter looked at the center of the food tray with her hands placed in front of her body.

Preliminary training. When Ayumu was 5 months old (155 days) preliminary training was conducted to achieve familiarization with the experimental setting. When Ayumu looked at the experimenter's face, the target object and social cue were presented. Three seconds after the cue, the experimenter presented food rewards independently of his behavior (a variation of the fixed-time schedule of reinforcement). There were seven such sessions, each consisting of five trials.

Experimental setting. At 7 months old (211 days), the experimental training started. When the subject looked at the experimenter's face, the experimenter presented a cue to the target object for 3 s, followed by the presentation of the food reward (a piece of fruit) through a hole in the tray nearest to the target object, independently of the subject's response (Fig. 2b).

We used four types of social cues as follows (Fig. 3):

- Tap. The experimenter gazed at and tapped the target object with an index finger.
- Point. The experimenter gazed at and pointed to the target object with an index finger. The distance between the finger and a target object was approximately 5 cm.
- Head turn. The experimenter turned her head and gazed toward the target object. The distance from the experimenter's head to the object was approximately 20 cm.
- Glance. The experimenter only glanced at a target object without any head turn. At the start of this condition, the experimenter gazed at the center of the food tray.

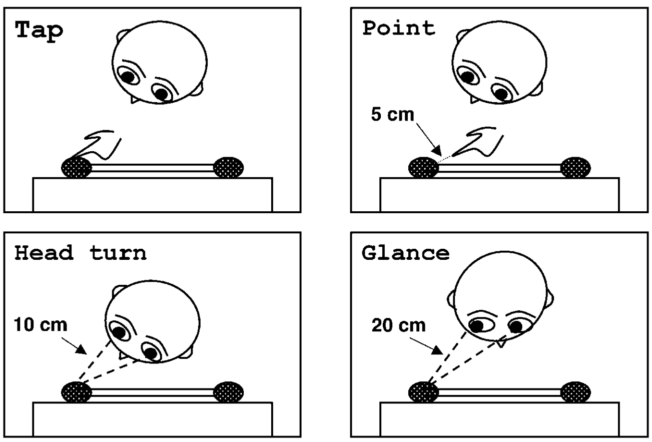

Fig. 3 The four types of cue conditions in experiment 1

Then she glanced at one of the objects back and forth, three times within 3 s. The distance from the experimenter's head to the object was approximately 20 cm. Furthermore, irrespective of the subject's response no food reward was presented: this condition was considered as the test for understanding of the social cues.

The subject also received three kinds of control (non-cued) trials, corresponding to each of the four types of social cues described above:

- Control 1. Passive face with the hands forming a fist at the midline between the two objects (four trials). This was the control condition for the tapping and pointing conditions.
- Control 2. Passive face, while jiggling the head from side to side at the midline between the objects (four trials). This was the control condition for gazing with head orientation.
- Control 3. Passive face with gazing at the center point and blinking repeatedly (four trials). This was the control condition for glancing.

For these 12 control trials per session, a food reward was presented as in the Tap, Point, and Head-turn conditions. The food reward was given through either the left or right hole according to a predetermined order irrespective of the subject's response.

Table 1 shows the design for experiment 1. The experimental training consisted of two phases. In the first phase (age 6.5–9.5 months), the subject was initially trained with the Tap cue, followed by the successive introduction of the Point and Head-turn cues. The Point cue was introduced in the fifth session, and the Head-turn cue was introduced in the tenth session. The number of trials per session during phase 1 is shown in Table 1. In the second phase (age 3.5–13.2 months), the Glance cue and control trials were introduced. In phase 2, each session comprised approximately 60 trials including baseline (Tap, Point, and Head-turn cues) trials. The Glance cues were presented on an average of 11 trials in a session (range 5–23 trials), depending on the subject's motivation. One session was conducted each week. In all conditions, the position of the target object (left or right) and the order of the conditions were randomized using Gellermann's (1933) random sequences. The target appeared equally often on the left and right sides. The acquisition criterion for each cued condition was 80% or more "follow" responses (see Data analysis) for two consecutive sessions.

Table 1 Number of trials for each cue condition per session and for each phase in experiment 1

Cue	Phase 1 Age			Phase 2
	211 days–	238 days–	281 days–	295 days–
Tap	20	20	20	10
Point		20	20	10
Head turn			20	20
Glance				11 (5–23)[a]
Controls (1–3)				12

[a]Mean number of trials (and range) in a session

Data analysis

The subject's responses were categorized into five types: (1) subject looks at the target object during cue presentation; (2) subject looks at the target object but only after the arrival of a reward; (3) subject looks at the experimenter's face; (4) subject does not look anywhere relevant; and (5) subject looks at the object on the side opposite to the target object during cue presentation. The first type of response was defined as "follow" and the latter four as "not follow". The experimenter categorized the subject's responses into these five types on the basis of video recordings. To assess inter-observer reliability, two additional observers also used the video recordings to judge the subject's response for a sample of four sessions. Observers were not informed which cues were presented. They judged whether the subject looked left or right instead of at the target or distracter object for categories 1, 2, and 5. Inter-observer reliability was computed by means of a Cohen's κ: κ=0.89.

All the present data stem from a single subject. In a strictly theoretical sense, it is inappropriate to use parametric and non-parametric tests for these non-independent data. However, the subject's responses in the Glance conditions were not differentially reinforced, so that one can assume that none of the trials were severely influenced by the previous trials' outcomes within a session. Thus, we used Fisher's exact probability tests and binomial tests for these data to determine whether gaze following occurred reliably using the number of "follow" and "not follow" responses in the trials for each session. The theoretical chance level for the binomial tests was set at 50% because we categorized the subject's responses into the two categories ("follow" and "not follow"). Furthermore, the performance for the Glance condition was compared with that for the control condition (indicating "actual" chance performances) by using Fisher's exact probability tests.

Results

Figure 4 shows the percentages of trials in which the subject made "follow" responses in each condition as a function of sessions and the subject's age. In the Tap condition, the subject scored 85% in the first session, and performance reached the criterion in the seventh session. In the Point condition, performance was initially 55.5% and reached criterion in four sessions. When the Head-turn condition was introduced, the subject's performance fluctuated during early sessions and become stable at approximately 80%. It took eight sessions to reach the criterion.

In phase 2, the subject's responses to these social cues were consistently accurate. Mean percentages of follow

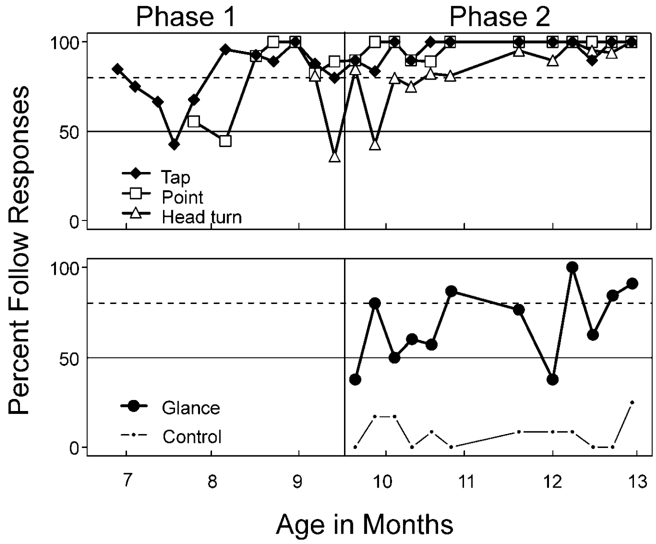

Fig. 4 Percentage of "follow" responses as a function of the subject's age in months

responses for the last six sessions were 98.3% for the Tap, 100% for the Point, and 95.6% for the Head-turn, respectively.

In control trials, the subject showed considerably fewer orienting responses. On average, he responded to the target object on 7.6% of trials, and to the side opposite to the predetermined location on 2.8% of trials. The results of each of the control conditions are shown in Table 2.

In the Glance condition, in which the non-reinforcement test was applied, the subject showed "chance" performance during the early sessions (57% averaged for the first 5 sessions). From the 6th session (before 11 months of age), the subject's performance gradually improved. Spearman's rank correlation between the sessions and performances (n=12) was r_s=0.558, and this value was significantly different from non-correlation, r_s=0 [P=0.0313, using a randomization test (Edgington 1987) on the basis of 100,000 random permutations].

Binomial tests revealed significant following to the Glance cue (all P<0.05) in the 6th, 7th, 9th, 11th, and 12th sessions (from under 11 months to 13 months of age). When we compared performance in control trials (the number of follow responses) using Fisher's exact probability tests, the subject showed significantly more "follow" responses in the Glance condition than in the control conditions in 10 of 12 sessions (all P<0.05), the exceptions being in the 3rd and 8th sessions. His performance reached criterion in the 12th session (13 months of age).

Note that in some sessions, the subject's performance was less accurate than in other sessions. For example, the subject was only slightly motivated by food in the fourth session in the Tap condition at the age of 231 days and showed a drop in performance. In contrast, in the eighth session in the Glance condition at the age of 365 days, the subject was very active and walked around inside the booth. The decrease of accuracy was limited to the Glance condition in this session, however: he showed accurate performance when the well-trained cue was presented.

Table 2 Results of control trials in experiment 1

	Look at the target (%)	Look at the opposite object (%)	Other (%)
Control 1	8.3	2.1	89.6
Control 2	10.4	2.1	87.5
Control 3	4.2	4.2	91.7
Average	7.6	2.8	89.6

Discussion

Experiment 1 clearly demonstrated that a chimpanzee infant less than 1 year old can reliably follow gaze cues by the human experimenter to shift his attention to a target object even when only the eye movements were given to the subject as social cues.

One of the procedural problems in this type of gaze-following task, however, is the difficulty in dissociating social cues and local-enhancement cues (Itakura et al. 1999). Local enhancement is defined as the shift of attention to the objects (or locations) that another individual has manipulated (Heyes 1993). Furthermore, non-social peripheral cues presented near the objects also capture the attention of both human infants and adults (Itakura 2001; Posner 1980; Matsuzawa and Shimojo 1997). It might be possible to interpret the present results on the basis of local enhancement or non-social peripheral cues. That is, the subject may have shifted his attention simply because the peripheral cues near the target captured his attention, not because he followed the "social" cues made by the human experimenter. This may be true especially for the Tap, Point, and Head-turn conditions. Both in the Point and Head-turn conditions, the distances between cues and target objects (approximately 5 cm) were shorter than in the Glance condition (see Figs. 2, 3).To rule out the possibility of local enhancement or non-social peripheral cues, we conducted a further experiment.

Experiment 2

Methods

Subject, apparatus, and stimuli

Infant chimpanzee Ayumu again served as subject in experiment 2. Ayumu was 17 months old at the beginning of experiment 2. The apparatus and stimuli were the same as in experiment 1.

Procedure

After experiment 1, follow-up training was continued from 14 months to 17 months of age. Each week one ses-

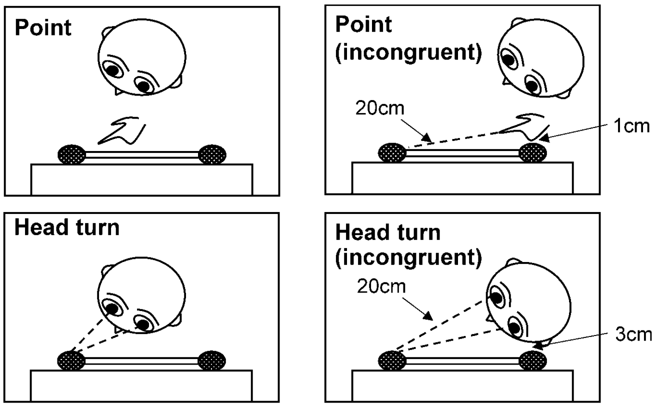

Fig. 5 The four types of cue conditions in experiment 2

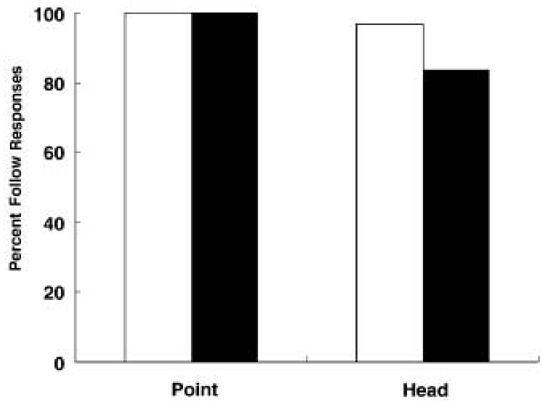

Fig. 6 Percentage of "follow" responses for each condition averaged across sessions in experiment 2. *Open bars* Congruent condition. *Solid bars* Incongruent condition

sion was conducted. The subject's responses to the previous social cues were consistently accurate. The mean percentages for the "follow" responses were 100% for the Tap, 99.2% for the Point, 96.1% for the Head-turn, and 81.6% for the Glance (non-reinforced) conditions, respectively.

After follow-up training, experiment 2 was initiated. The experimental procedure was the same as in experiment 1 but we did not present the Tap and Glance cues. In addition to the Point and Head-turn cues, we used two new types of cues as follows (Fig. 5):

- Incongruent point. The experimenter gazed at and pointed to the target object with an index finger from the side of the other object (distracter). The distance between the knuckle and the distracter object was approximately 1 cm, and that between the finger and the target object was approximately 20 cm.
- Incongruent head turn. The experimenter oriented head and eyes toward the target object from the side of the distracter object. The distances between the head and the target and distracter object were approximately 20 cm and 3 cm, respectively.

The social and local-enhancement properties of these incongruent cues indicated the different objects. If the subject mainly used the local-enhancement property, he would select the distracter object. In contrast, if he attended to the social property of these cues, he would orient to the target object. In both incongruent cueing conditions, no food reward was presented irrespective of the subject's response, so that these conditions were considered as a test for the understanding of the social cues.

Each session consisted of 40 trials including 14 Point and 14 Head-turn trials, and 6 Incongruent point and 6 incongruent Head-turn trials. One session was conducted each week and two sessions were given to the subject.

Data analysis

Data analysis was conducted in the same manner as in experiment 1. Two additional observers (not informed about the cues) also judged the subject's response using the video recordings to assess inter-observer reliability, calculated for a sample of one session. Inter-observer reliability was 0.90 (Cohen's κ).

Results and discussion

Figure 6 shows the percentage of follow responses for each condition averaged across two test sessions. In both the normal Point and Head-turn conditions, the subject showed highly accurate performances, 100% for the Point and 96.9% for the Head turn. Furthermore, Ayumu looked significantly more often at the socially cued object (target) in both the incongruent conditions: 100% for the Incongruent point condition (12/12, follow/total, $P<0.01$, binomial test) and 83.3% for the Incongruent head-turn condition (10/12, $P<0.05$).

These results clearly show that the subject's performance was controlled by the "social" properties (orientation of the finger tip or head) of the experimenter-given cues but not by the non-social, local-enhancing peripheral properties.

General discussion

The results of the two experiments clearly demonstrate that a chimpanzee infant less than 1 year old can reliably follow the gaze cues given by a human experimenter to shift his attention to a target object. This behavior was not controlled by the non-social peripheral property (or local enhancement) of the experimenter-given cues. Unfortunately, we only tested a single chimpanzee infant in this study. Thus, tests with more subjects are needed to verify the generality of the present results. Nevertheless, the present results have many implications for comparative research on gaze following.

It has previously been reported that infant chimpanzees less than 3–4 years old do not use head-turn cues (Tomasello et al. 2001). Contrary to this result, our subject reliably used "head turn" as a cue at 11 months and "glance" at 13 months of age. One possible reason for this inconsistency might be differences in the experimental settings. In Tomasello et al.'s study, the experimenter looked up to the sky or the ceiling, whereas in the present study, the experimenter looked at the toy as a target object in the subject's visual field. A more important point is that these procedures focus on different aspects of joint visual attention. As mentioned in the introduction, Butterworth and Jarrett (1991) reported three successively emerging mechanisms of joint visual attention in human infants from 6 to 18 months. In the present study, we used a specific object within the subject's visual field as a target. This procedure investigates the ecological or geometric mechanism of joint visual attention. Tomasello et al.'s study, on the other hand, used no specific objects, but subjects were required to move their heads or bodies. This procedure may require a representational mechanism. Tomasello et al. (1999) reported that chimpanzees follow the gaze direction of other individuals to specific locations geometrically, in much the same way as human infants do. Our experiment used only two specific locations in the subject's visual field. This procedure might be insufficient for distinguishing between the ecological and geometric mechanisms (see Butterworth and Jarrett 1991). To address problems concerning the underlying mechanisms of gaze following in chimpanzee infants, we need further experimental manipulations, for example, a greater number of specific locations for the target.

In the present experiment, the infant followed the glance cues without explicit differential reinforcement training by 13 months of age. Povinelli and Eddy (1996) reported that chimpanzees 5–6 years old responded appropriately both to head turns and eye movement alone. Itakura and Tanaka (1998) also reported that adult chimpanzees can use eye movement as a cue in object-choice tasks. However, with the exception of the present study, there has been no evidence that infant chimpanzees can use eye movements alone as a cue. Human infants at 9 months of age are unable to shift attention by glance cues without head turning. At 12 and 14 months of age, half of the subjects can shift their attentions using glance cues (Lempers 1979; Butterworth and Jarrett 1991; but see also Corkum and Moore 1995). These ages apparently correspond to the chimpanzee infant in the present study. However, it is well known that the speed of body growth and perceptual development in chimpanzees is approximately twice as fast as that of humans. We need further studies both in humans and chimpanzees to draw clear conclusions concerning the onset of gaze-following abilities.

It is necessary to verify both geometric and representational mechanisms in young chimpanzees. From what age can young chimpanzees look back to the target? It is necessary to conduct a more detailed examination of the concept of gaze following and joint visual attention. Such studies will provide a clearer idea of visual communication including joint visual attention and the understanding of social-cognitive abilities in non-human primates.

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References

Anderson JR, Mitchell RW (1999) Macaques but not lemurs co-orient visually with humans. Folia Primatol (Basel) 70:17–22
Butterworth G, Cochran E (1980) Towards a mechanism of joint visual attention in human infancy. Int J Behav Dev 3:253–272
Butterworth G, Jarrett NLM (1991) What minds have in common is space: spatial mechanism serving joint visual attention in infancy. Br J Dev Psychol 9:55–72
Call J, Hare BA, Tomasello M (1998) Chimpanzee gaze following in an object-choice task. Anim Cogn 1:89–99
Corkum V, Moore C (1995) Development of joint visual attention in infants. In: Moore C, Dunham PJ (eds) Joint attention: its origins and role in development. Erlbaum, Hillsdale, N.J., pp 61–83
Edgington ES (1987) Randomization test, 2nd edn. Dekker, New York
Emery NJ, Lorincz EN, Perrett DI, Oram MW, Baker CI (1997) Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). J Comp Psychol 111:286–293
Ferrari PF, Kohler E, Gallese V (2000) The ability to follow eye gaze and its emergence during development in macaque monkeys. Proc Natl Acad Sci U S A 97:13997–14002
Gellermann LW (1933) Chance orders of alternating stimuli in visual discrimination experiments. J Genet Psychol 42:207–208
Heyes CM (1993) Imitation, culture and cognition. Anim Behav 46:999–1010
Holden C (2001) Like mother, like son. Science 292:205
Itakura S (1996) An exploratory study of gaze-monitoring in non-human primates. Jpn Psychol Res 38:174–180
Itakura S (2001) Attention to repeated events in human infants (*Homo sapiens*): effects of joint visual attention versus stimulus change. Anim Cogn 4:281–284
Itakura S, Anderson JR (1996) Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. Curr Psychol Cogn 15:103–112
Itakura S, Tanaka M (1998) Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*) and human infants (*Homo sapiens*). J Comp Psychol 112:119–126
Itakura S, Agnetta B, Hare B, Tomasello M (1999) Chimpanzee use of human and conspecific social cues to locate hidden food. Dev Sci 2:448–456
Kawai N, Matsuzawa T (2000) Numerical memory span in a chimpanzee. Nature 403:39–40
Lempers JD (1979) Young children's production and comprehension of nonverbal deictic behaviors. J Genet Psychol 135:93–102
Matsuzawa M, Shimojo S (1997) Infants' fast saccades in the gap paradigm and development of visual attention. Infant Behav Dev 20:449–455
Matsuzawa T (2001a) The baby and Ai (in Japanese). Kodansha, Tokyo

Matsuzawa T (2001b) Primate origins of human cognition and behavior. Springer, Berlin Heidelberg Tokyo
Myowa-Yamakoshi M, Tomonaga M (2001) Perceiving eye gaze in an infant gibbon (*Hylobates agilis*). Psychologia 44:24–30
Peignot P, Anderson JR (1999) Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. J Comp Psychol 113:253–260
Posner MI (1980) Orienting of attention. Q J Exp Psychol 32:3–25
Povinelli DJ, Eddy TJ (1996) Chimpanzees: joint visual attention. Psychol Sci 7:129–135
Povinelli DJ, Eddy TJ (1997) Specificity of gaze-following in young chimpanzees. Br J Dev Psychol 15:213–222
Primate Research Institute, Kyoto University (1986) Guide for the care and use of laboratory animals. Kyoto University, Kyoto, Japan
Scaife M, Bruner JS (1975) The capacity for joint visual attention in the infant. Nature 253:265–266
Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics. Anim Behav 55:1063–1069
Tomasello M, Hare B, Agnetta B (1999) Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. Anim Behav 58:569–777
Tomasello M, Hare B, Fogleman T (2001) The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. Anim Behav 61:335–343
Tomonaga M (1999) Attending to the others' attention in macaques: joint attention or not? (in Japanese) Primate Res 15:425
Tomonaga M, Myowa-Yamakoshi M, Terazawa N (2000) Gaze recognition in nonhuman primates (in Japanese). In: Annual Research Report of the Grant-in-Aid from the Ministry of Education, Culture, Sports and Science "Development of Mind." Ministry of Education, Culture, Sports and Science, Tokyo, pp 28–33
Vick SJ, Anderson JR (2000) Learning and limits of use of eye gaze by capuchin monkeys (*Cebus apella*) in an object-choice task. J Comp Psychol 114:200–207