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PAPER

Development of using experimenter-given cues in infant chimpanzees: longitudinal changes in behavior and cognitive development

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Abstract

The use of gaze shifts as social cues has various evolutionary advantages. To investigate the developmental processes of this ability, we conducted an object-choice task by using longitudinal methods with infant chimpanzees tested from 8 months old until 3 years old. The experimenter used one of six gestures towards a cup concealing food; tapping, touching, whole-hand pointing, gazing plus close-pointing, distant-pointing, close-gazing, and distant-gazing. Unlike any other previous study, we analyzed the behavioral changes that occurred before and after choosing the cup. We assumed that pre-choice behavior indicates the development of an attentional and spatial connection between a pointing cue and an object (e.g. Woodward, 2005); and post-choice behavior indicates the emergence of object permanence (e.g. Piaget, 1954). Our study demonstrated that infant chimpanzees begin to use experimenter-given cues with age (after 11 months of age). Moreover, the results from the behavioral analysis showed that the infants gradually developed the spatial link between the pointing as an object-directed action and the object. Moreover, when they were 11 months old, the infants began to inspect the inside of the cup, suggesting the onset of object permanence. Overall, our results imply that the ability to use the cues is developing and mutually related with other cognitive developments. The present study also suggests what the standard object-choice task actually measures by breaking the task down into the developmental trajectories of its component parts, and describes for the first time the social-physical cognitive development during the task with a longitudinal method.

Introduction

By the end of their first year, human infants are sensitive to information specifying where others are looking. The ability to follow the gaze of other individuals is a critical component of joint attention, defined as looking toward the object of others' attention. Infants show a specific developmental trajectory in this ability. Before 12 months of age, human infants follow their mother's gaze, but do not direct their attention to the object of her attention. At around 12 months, infants begin to follow their mother's gaze towards particular objects in their visual field and at around 18 months they can direct their attention to objects outside of their visual field (e.g. Scaife & Bruner, 1975; Butterworth & Cochran, 1980; Butterworth & Jarrett, 1991; Corkum & Moore, 1995; D'Entremont, Hains & Muir, 1997). Joint attention is considered an early social cognitive ability leading to the later development of the ability to infer others' mental states (cf. Baron-Cohen, 1995; Tomasello, 1995).

However, eye gaze is not the only attentional cue. The orientation of the whole head, body, and hand (e.g. pointing) are similarly good indicators of attention and interest, and are used in our daily interactions with others. Pointing, in particular, is considered an important component of joint attention as an indicator of particular objects, locations, or events. At about 12 months, infants begin to follow pointing to distant locations. Before 12 months, infants are likely to ignore pointing or look at the pointing hand itself (Butterworth & Jarrett, 1991; Desroachers, Morissette & Ricard, 1995; Lempers, 1979; Leung & Rheingold, 1981; Murphy & Messer, 1977). However, if pointing occurs in physical contact with the referred to object, or close proximity to the object, it may also function as a spotlight of attention for younger infants as young as 9 months of age and facilitate looks to the object (Lempers, 1979; Murphy & Messer, 1977). Woodward and colleagues (Woodward & Guajardo, 2002; Woodward, 2005) suggest that by 12 months, infants seem to understand pointing (in this case it was

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'touching' the object with the index finger) as an object-directed action.

Gaze following is also found in a number of non-human primates. The use of gaze shifts as social cues has various evolutionary advantages. For instance, gaze shifts may index the location of predators, potential mates or food sources. Several field studies suggest that primates follow the gaze of conspecifics (e.g. Chance, 1967; Menzel & Halperin, 1975; Whiten & Byrne, 1988). A number of laboratory studies have also investigated the behavior of gaze following. Two common methods have been used to investigate non-human primates' ability to use social cues such as gaze; investigate whether a given species of primates follows another individual's gaze (gaze following task) and whether it is able to use gaze as a cue within an object-choice task. The clearest evidence for the ability to follow gaze in non-human primates comes from laboratory work on great apes, in particular, studies with chimpanzees.

Within a gaze following task paradigm, various studies with chimpanzees have demonstrated that they follow the gaze direction of other individuals (see e.g. Itakura, 1996; Povinelli & Eddy, 1996; Tomasello, Call & Hare, 1998; Emery, 2000, for reviews). Additionally, previous studies from a developmental perspective reported that by 13 months of age, an infant chimpanzee showed reliable following responses to the object that was indicated by various cues, including glancing alone. From 21 months of age, the infant started to look back at the target behind him (Okamoto, Tomonaga, Ishii, Kawai, Tanaka & Matsuzawa, 2002; Okamoto, Tanaka & Tomonaga, 2004). Although there are some developmental differences about the onset of each 'level' of gaze following (e.g. Okamoto *et al.*, 2004), on the surface, the development of gaze following in human and chimpanzee infants appears to be highly similar.

In the other common method, the 'object-choice task', subjects must choose one of two containers, of which only one is baited. Anderson and his colleagues used this task for measuring the sensitivity to social cues in primates. In a series of studies, they investigated the ability of capuchin monkeys (Anderson, Sallaberry & Barbier, 1995) and rhesus macaques (Anderson, Montant & Schmitt, 1996) to utilize human attention cues to gain food rewards in a Wisconsin General Testing Apparatus (WGTA). An experimenter presented different cues to the subjects: 'pointing only', 'gaze only' (head orientation and eyes cues) and 'gaze and pointing'. None of the capuchin monkeys or macaques could be trained to use the 'gaze only' cue to guide their responses. Two subjects of each species could be trained to use either 'pointing only' or 'gaze and pointing'. Additionally, after extensive training, capuchin monkeys were able to also use gaze cues in addition to tap and point cues, but only if the gaze cue included eye and head movement (Itakura & Anderson, 1996; Vick & Anderson, 2000).

Using a similar paradigm, Itakura and Tanaka (1998) found that chimpanzees, an enculturated orangutan and human infants (18–27 months old) used all cues, including tapping, pointing, gazing (head turning) and glancing (without head turning), to choose the baited container. The responses of all subjects appeared to be spontaneous, not requiring learning. Other previous studies also reported that chimpanzees, orangutans and a gibbon were able to find the reward indicated by different communicative cues, including eyes-only cues (Itakura & Tanaka, 1998; Call, Hare & Tomasello, 1998; Inoue, Inoue & Itakura, 2004). However, in some studies, chimpanzees (e.g. Tomasello, Call & Gluckman, 1997; Itakura, Agnetta, Hare & Tomasello, 1999) as well as gorillas (Peignot & Anderson, 1999) were unable to use eye direction alone to locate the baited container. These differences may be due to the experimental experience and testing design (cf. Barth, Reaux & Povinelli, 2005), and enculturation (e.g. developmental history) of the different groups of primates. Overall, it is likely that non-human primates have some difficulties in using gaze cues in the object-choice task (see also Itakura & Anderson, 1996; Call & Tomasello, 2005) as compared to humans.

Previous studies using the object-choice task, however, have tested adult (or juvenile) subjects to investigate the ability to use gaze cues. From which age this ability develops is still an open question. A longitudinal study of infant chimpanzees that measures the emergence of the ability to use gaze cues in the course of development may yield important clues as to the ontogeny of this behavior.

Moreover, a pointing gesture which is using only the index finger, a repertoire of social cues that has been used in previous studies, could be considered a stereotyped species-typical gesture of humans. Captive chimpanzees point by extending their whole arm and stretching all fingers (whole-hand pointing) rather than by using their index finger only in their interaction with humans (Leavens & Hopkins, 1999; Parr & Maestripieri, 2003). This gesture has been observed in all four species of great apes, and in some species of monkeys as well (Leavens & Hopkins, 1999). This behavior is generally observed in the context of requests for food towards humans (see Parr & Maestripieri, 2003, for a review). Thus, previous research lacked an assessment of the chimpanzees' ability to use their frequent communicative repertoire towards humans. Whether infant chimpanzees can use 'whole-hand pointing', and comparing their use of index finger pointing and whole-hand pointing, is an important facet in terms of investigating the emergence of their ability to use social cues for finding hidden foods.

Unlike a simple gaze following task which mainly requires natural following responses, the object-choice task requires additional skills of the animals to perform the task successfully. First, the animals should follow the behavioral cues of another individual. This might require the ability to follow the other's gaze or pointing and an understanding of these behaviors as object-directed or communicative actions. If infants lacked an understanding of gaze and pointing as object-directed actions, it would be impossible for them to interpret these behaviors as anything more than a series of motions (Woodward, 2005). For instance, the pointing gesture from a close distance is often used in natural interactions between human mother and infant when communicating about objects (e.g. Desrochers *et al.*, 1995). As we mentioned before, previous research suggested that pointing may function as a spotlight of attention for human infants and facilitate looking behavior to the object (Lempers, 1979; Murphy & Messer, 1977; Woodward, 2005). These reports suggest that there is a stage when infants begin to have the attentional connection between a pointing cue and an object. From the developmental perspective of comprehension of pointing, it is important to investigate how the infants' looking behavior and their actual performance change over time.

Second, the infants should be aware that a piece of reward continues to exist under one of the containers even when it is no longer visible. This assumption is related to one of the cognitive developmental milestones, 'object permanence' (Piaget, 1954). Jean Piaget conducted experiments with human infants which led him to conclude that object permanence was typically achieved around 7 to 8 months, during the sensorimotor stage of cognitive development. This cognitive skill emerges in human infants through a fixed series of steps with characteristic transitional errors and has been investigated by numerous investigators (see Schuberth, 1983, for a review). A number of researchers (e.g. Bower, 1974; Baillargeon, Spelke & Wasserman, 1985) have suggested that young infants' failure to search for hidden objects results not from a lack of object permanence but from an inability to perform coordinated actions. These researchers conducted a study which does not require manual search for assessing acquiring object permanence and reported that much younger infants than in Piaget's study showed emergence of this skill (see Bower & Wishart, 1972; Bower, 1974; Baillargeon *et al.*, 1985; Baillargeon, 1995, for reviews). Comparative research also shows that many species develop object permanence skills in exactly the same sequence as human infants but at different speeds. Apes are slightly faster than humans in all steps (see Gómez, 2004, 2005, for reviews). In any case, it is important to consider the infants' manual search in terms of coordinated action sequence during the object-choice task. We need to split this action into two separate actions; one upon the cup (occluder) and one upon the food (object).

In sum, to investigate the developmental time course of the ability to use social cues, we should focus on the development of these other cognitive and physical abilities. The present study with infant chimpanzees investigated the emergence and development of the ability to use social cues provided by an experimenter. We introduced an object-choice task paradigm based on the one used in Itakura and Tanaka (1998). Most importantly, unlike any other previous studies, we analyzed the behavioral changes that come with age by classifying the behaviors during performance in the task into two phases; *before* choosing the cup and *after* choosing the cup. We assumed that behavioral analysis of pre-choice behavior might show when chimpanzee infants begin to have the attentional connection between a pointing cue and an object. Furthermore, behavioral analysis of post-choice behavior might show the emergence of their understanding of object permanence which requires manual action. The present study breaks the object-choice task down into the developmental trajectories of its component parts, and the behavioral analysis describes for the first time the social/physical cognitive development (the attentional connection between a person and an object [e.g. Woodward, 2005], and object permanence [e.g. Piaget, 1954]), and physical development during the task with a longitudinal method. We started to introduce the task from 6 months old for habituation to the testing situation, and conducted testing from 8 months old until 3 years old.

Method

Subjects

We studied three chimpanzee infants, a male named Ayumu, and two females named Cleo and Pal (from 8 months old until 3 years old). All infants had been reared with their biological mothers since birth at the Primate Research Institute, Kyoto University (PRI). They lived in an enriched outdoor compound in a community of 14 chimpanzees (Ochiai & Matsuzawa, 1998). All infants had participated in a research project on chimpanzee development which started in 2000 and therefore had experienced a variety of tests related to the development of cognitive abilities (e.g. Matsuzawa, 2003; Matsuzawa, Tomonaga & Tanaka, 2006; Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa, 2003; Tomonaga, Tanaka & Matsuzawa, 2003; Tanaka, Tomonaga & Matsuzawa, 2003; Matsuzawa, 2007). The infants had not received a test which was directly related to the present study (use of gaze and pointing cues, and object permanence). Only Ayumu had received a gaze following task (e.g. Okamoto *et al.*, 2002). Their mothers had also participated in cognitive experiments (e.g. Matsuzawa, 1985; Tanaka, 1997; Tomonaga, 1998; Kawai & Matsuzawa, 2000). Care and use of the chimpanzees adhered to the *Guide for the care and use of laboratory primates* (2002) of the Primate Research Institute, Kyoto University.

Experimental setting

The experiment was conducted in a testing booth at the PRI (see Figure 1). The experimental apparatus consisted of a wooden board (15 × 40.5 cm) and two identical blue, opaque, and inverted aluminum cups (height, 5 cm; diameter of top, 4.5 cm; diameter of bottom, 6.5 cm). The cups were mounted on a board (the

Figure 1 *The chimpanzee infant is performing the task (with permission from* The Mainichi *Newspaper, Japan).*

distance between the cups was approximately 34 cm) and were used to cover the food reward (e.g. a piece of fruit) on each trial. The cups could be opened by the chimpanzees to take a reward hidden in one of them. The experiment was conducted by three experimenters. The main experimenter A was in the testing booth with the subject and executed the experiment. Experimenter B filmed the whole experiment from outside the booth, and experimenter C scored the subject's responses on each trial. All subjects were highly familiar with the testing booth and experimenter A because they regularly visited the booth and had interacted with experimenter A since their birth. The behavior of the infant was continuously recorded by two video cameras (DV cameras [SONY DCR-TRV950]).

Procedure

To assess developmental changes in using experimenter-given cues, the chimpanzees were tested once a week from 8 months old until 3 years old. We invited a mother–infant pair to enter the experimental booth. Experimenter A sat face-to-face with the subject during the experiment (the initial distance between them was approximately 80 cm). The baiting procedure was hidden from the subject's view by the experimenter turning his back to the infants when he was preparing the trial. After the baiting procedure, the experimenter started a trial by turning back to the subject again and placing the board in front of the subject according to their height (approximately 25 cm from the floor depending on body size). At the onset of a trial, the experimenter gained the subject's attention (e.g. by calling their name). Once the subject looked at the experimenter, he gave one of the cues to the correct cup. After giving a cue, the subjects were allowed to respond by displacing one of the two cups with their hands. For choosing and opening the cup, the infants walked to the board. When the subjects chose the correct cup which included a food reward, they could retrieve and eat it. When the subjects chose the wrong cup, the experimenter withdrew the board and the trial ended. The subjects were allowed to respond to only one cup per trial. Inter-trial intervals were approximately 20 seconds.

Prior to the testing phase, we introduced a pre-training phase in which the subjects could become familiar with the task and testing apparatus from when they were 6 months old. For this orientation, we introduced two settings (1) transparent cups in which they could see the contents of the cups and (2) a procedure in which the experimenter showed the baiting procedure with opaque testing cups. This phase was implemented to facilitate the infants' practice of manipulating the cups, and increasing their motivation to choose the cups and receive food rewards from the board. During this training phase, even when the subjects did not choose the correct cup, occasionally the cup was displaced and the infants could take the food reward from the board. On every trial, the infant could see the food reward during the procedure. This setting allowed us to train the infant to learn that there is a reward on the board in every trial. This pre-training phase consisted of a session of six trials and was conducted once a week. The testing phase started from when they were 8 months old. The infants began to show a spontaneous object manipulation at around this age (Hayashi & Matsuzawa, 2003). In the testing phase, we administered seven conditions as follows:

Tap: The experimenter gazed at and tapped on the correct cup with his index finger.
Touch: The experimenter gazed at and touched the correct cup with his index finger.
Whole-hand point: The experimenter gazed at and extended his arm to the correct cup while stretching all fingers. The fingers spread apart slightly and the palm held pronated to some degree (Leavens & Hopkins, 1998). The distance between the finger and the correct cup was approximately 5 cm.
Close-point: The experimenter gazed at and pointed to the correct cup with an index finger. The distance between the finger and a correct cup was approximately 5 cm.
Distant-point: The experimenter gazed at and pointed to the correct cup with an index finger. The distance between the finger and a correct cup was approximately 20 cm.
Close-gaze: The experimenter oriented his head and eyes toward the correct cup, approximately 10 cm from the cup.
Distant-gaze: The experimenter oriented his head and eyes toward the correct cup, approximately 50 cm from the cup.

The initial orientation of the experimenter's gaze was towards the subject in all conditions. The cues remained static when given and were maintained until a choice was made except for tapping and touching conditions.

Each session consisted of eight trials, and the session was conducted once a week. The location of the correct side (left or right) was counterbalanced in each session. The acquisition criterion for each cue was 13 or more correct responses (more than 80% correct responses) for two consecutive sessions (16 trials in total) (Ogawa, 1989; Itakura & Tanaka, 1998). A score of 13 or more correct responses for two consecutive sessions (above 6/8 for each session and overall 13/16 across two consecutive sessions) represents a performance significantly above chance ($p < .05$) by using a binomial test with a chance level of 50%. However, correct responses in six or more trials per session were required.

The subjects' choices were scored during the experiment by experimenter C within two straightforward categories; *correct* (the subject opened and displaced the cup that concealed the reward) or *incorrect* (the subject opened and displaced the empty cup).

Behavioral analysis; before choosing the cup

We focused on the close-point condition for two reasons. First, this condition is most informative in terms of investigating when infants begin to have the attentional connection between a social cue and an object (e.g. Woodward, 2005). Second, all three infants received this condition, and reached criterion after a comparable amount of trials. This situation allowed us to track the subjects' developmental changes from their early stages until they reached criterion. Other cue conditions did not meet the requirements for this analysis. For instance, in the Tap and Touch conditions, the experimenter's finger cues did not remain during the infant's choices, because it might distract the infants' responses if the experimenter keeps tapping or touching the cup during the infant's response. Moreover, the infants required different numbers of trials in the whole-hand pointing condition and the distant-point condition. In both gaze conditions, one infant did not reach the criterion even after a large number of trials.

We classified the infants' behaviors before choosing the cup into three categories; the subject (a) looks at the experimenter's pointing (close distance condition) and chooses the correct cup, (b) looks at the experimenter's pointing and chooses the incorrect cup, and (c) does not look at the experimenter's pointing and chooses any cup. The infant's first look was coded once the close-point cues were given.

The main observer classified the subjects' behaviors, according to the categories described above, from the video recordings. To assess inter-observer reliability, an additional coder watched 50% of all video recordings and rated the subjects' behavior after training in coding. The main rater and the second rater agreed on 88% of the trials (176/200), resulting in a kappa coefficient of $\kappa = .81$.

Behavioral analysis; after choosing the cup

We classified the infants' first sequential response into three different categories: the subject (A) picks up the cup, and then only looks at or manipulates the cup (including bringing the cup to the mouth), (B) picks up the cup, and then looks at the location where the cup was, or looks inside the cup when there is no reward on the board, (C) picks up the cup, and then leaves the cup and also does not look at the board and cup at all. For following the developmental changes with age, we analyzed one session per month (the session which is the closest one to the date of the birth of each subject [Ayumu; 24th, Cleo; 19th, Pal; 9th]) from the beginning of the experiment (8 months old) until 18 months old irrespective of the condition and choice made (correct or incorrect). Thus behavior (A) simply shows their interest in the cup itself, but not the food reward which is no longer visible. Then, once removing the cup, as a consequence, if they saw the food reward ('accidentally'), they usually ate it. But if there was no food reward on the board, they simply kept focusing on the cup and just continued to play with it. In other words, the presence of the food reward basically did not change their behavior after choosing the cup except when they saw the food as a success consequence (they might not expect to find food under the cups). However, behavior (B) represents a different stage of their cognitive development. The infants' motives are focused on removing the cup to find the reward under the cup. If they were successful on a trial, they saw the reward on the board and ate it. If they failed to use the cues to find the correct cup, they looked at the location where the cup was, and looked inside the cup. The age at which they start to show this behavior (B) indicates the emergence of object permanence which requires manual action in this case. Lastly, behavior (C) simply shows a lack of motivation towards the task.

The main observer classified the subjects' behaviors, according to the categories described above, from the video recordings. To assess inter-observer reliability, an additional coder watched 50% of all video recordings and rated the subjects' behavior after training in coding. The main rater and the second rater agreed on 90.2% of the trials (119/132), resulting in a kappa coefficient of $\kappa = .84$.

Results

Development of using the experimenter-given cues

Figure 2 shows the age in months at which the infants reached criterion for each condition. Table 1 shows the number of trials until acquiring the criterion and the age at which the infants started each condition. When the infants showed gradual development over time after a number of trials or retention of acquaintance of the criterion, another cue condition (next step or one step back, see Table 1) was presented in parallel for determining the precise starting age for each cue. At around 11 months, the infants (Ayumu; 11 months old, 104 trials [13 sessions] and Pal; 12 months old, 80 trials

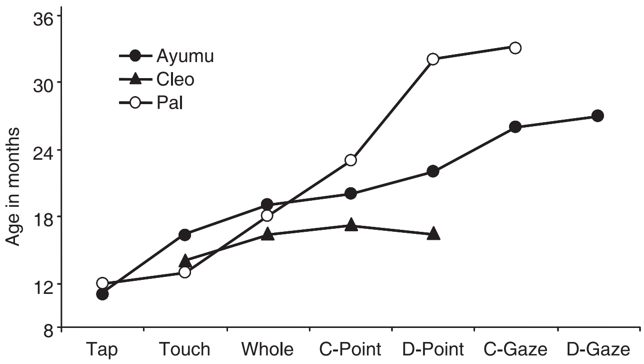

Figure 2 *The age at which the infants reached criterion in each condition.*

Table 1 *The age at which the infants started and reached criterion in each condition (m; months old) and the number of trials until acquiring criterion. Started age in months (m): criterion acquired age (m) [number of trials required]*

Cues	Ayumu	Cleo	Pal
Tap	8 m: 11 m [104]	–	8 m: 12 m [80]
Touch	15 m: 16 m [16]	13 m: 14 m [16]	12 m: 12 m [16]
Whole-Hand	18 m: 18 m [16]	15 m: 16 m [32]	15 m: 17 m [56]
C-Point	12 m: 19 m [112]	8 m: 17 m [120]	12 m: 23 m [168]
D-Point	17 m: 21 m [32]	16 m: 16 m [16]	18 m: 32 m [96]
C-Gaze	21 m: 25 m [64]	22 m: – [264]	20 m: 33 m [80]
D-Gaze	25 m: 26 m [24]	–	–

[10 sessions]) reached criterion in the tap condition. However, they reached criterion in the touch condition very quickly (Ayumu; 16 months old, 16 trials [two sessions], Cleo; 14 months old, 16 trials [two sessions], Pal; 12 month old, 16 trials [two sessions]). The whole-hand point condition was introduced because the subjects had difficulty reaching criterion in the close-point condition. The infants reached criterion in this condition within relatively few sessions (Ayumu; 18 months old, 16 trials [two sessions], Cleo; 16 months old, 32 trials [four sessions], Pal; 17 months old, 56 trials [seven sessions]). In contrast, for reaching criterion in the close-point condition, all three infants needed large numbers of sessions (Ayumu; 19 months old, 112 trials [14 sessions], Cleo; 17 months old, 120 trials [15 sessions], Pal; 23 months old; 168 trials [21 sessions]). Cleo received the point-close condition from the beginning of the experiment (8 months old). However, she needed approximately the same number of trials as Ayumu for reaching criterion. In contrast to the close-point condition, the infants acquired criterion in the distant-point condition in relatively few sessions (Ayumu; 21 months old, 32 trials [four sessions], Cleo; 16 months old, 16 trials [two sessions], Pal; 32 months old, 96 trials [12 sessions]). Note that irrespective of age, all infants acquired criterion in both the close- and the distant-point condition after meeting the criterion in the whole-hand point condition. Two of the infants acquired criterion in the close-gaze condition (Ayumu, 25 months old, 64 trials [eight sessions]; Pal, 33 months old, 80 trials [10 sessions]). Even after a large number of sessions (264 trials [33 sessions]), Cleo did not reach criterion in the close-gaze condition. Only Ayumu reached criterion in the distant-gaze condition (26 months old, 24 trials [three sessions]). In sum, the infant chimpanzees began to use the experimenter-given cues such as tapping and touching when they were approximately 1 year old. They started to use the pointing (close-point) cue before they were 2 years old. They used the whole-hand pointing cue before they started to use the index finger pointing. Two of them started to use the gaze (close-gaze) cue after they turned 2 years old. Only one infant reached criterion in the distant-gaze condition, just after reaching criterion in the close-gaze condition.

Behavioral changes during the experiment; before choosing the cup

We analyzed the developmental changes that occurred in the subjects' choice behavior from the perspective of a triadic relationship between the close-point cues, the cups and the infants' looking behavior; (a) looks at the experimenter's pointing (close-distance condition) and chooses the correct cup, (b) looks at the experimenter's pointing and chooses the incorrect cup, (c) does not look at the experimenter's pointing and chooses any cup. Behavioral sequence (a) represents the appropriate behavioral sequence to make a correct choice and reach criterion and eventually shows that there is an attentional link between the pointing cue and the cup. Behavioral sequence (b) represents lacking an attentional link between the pointing cue and the cup.

Figure 3 shows the behavioral changes before choosing the cup during the experiment as a function between age and time until the subjects reached criterion. Ayumu required 14 sessions from 12 months old until 19 months old. Cleo required 15 sessions from 8 months old until 17 months old. Pal required 21 sessions from 12 months old until 23 months old. Although each infant required different numbers of trials for reaching criterion, they showed a consistent pattern in their behavioral changes. Behavioral category (b), looking at the pointing cue and choosing the incorrect cup, which shows a lack of understanding of the spatial and attentional link between the pointing and the cup disappeared gradually with age (Spearman's correlation test; Ayumu: $r_s = 0.57$; $n = 14$; $p < .05$, Cleo: $r_s = 0.69$; $n = 15$; $p < .01$, Pal: $r_s = 0.80$; $n = 21$; $p < .001$) so that they reached criterion (Cleo; 16 months, Ayumu and Pal; 19 months old). This disappearance of behavior (b) implies that the subjects gradually developed the awareness and understanding of the attentional connection between the pointing cue (or pointer) and the object in their environment.

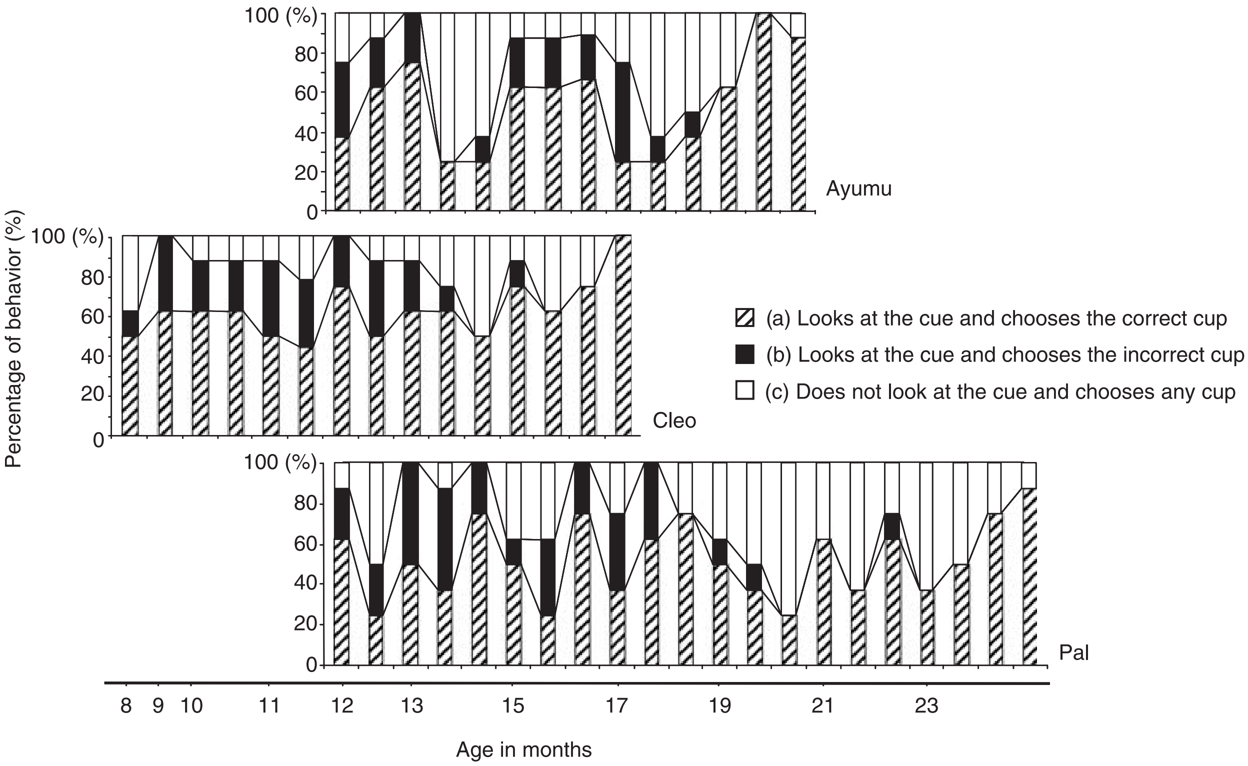

Figure 3 *The percentage of each categorized behavior as a function of session and the subject's age.*

Behavioral changes during the experiment; after choosing the cup

We analyzed the behavioral sequence after choosing the cup from the perspective of the behavior which is related to the object (cup and food reward): the subject (A) picks up the cup, and then only manipulates the cup (including bringing the cup to the mouth), (B) picks up the cup, and then looks at the location where the cup was, or looks inside the cup when there is no reward on the board, (C) picks up the cup, and then leaves the cup and also does not look at the board and cup at all.

Figure 4 shows the mean percentage of the three infants' behavioral changes after choosing the cup during the experiment as a function of age. We split the data into before (8 to 12 months old) and after (13 to 18 months old) 12 months for statistical analysis. The behavior of all three infants significantly changed after 1 year old (Ayumu; $\chi^2(2) = 44.28$, $p < .001$, Cleo; $\chi^2(2) = 34.60$, $p < .001$, Pal; $\chi^2(2) = 32.74$, $p < .001$). At the beginning of the experiment, the infants showed behaviors (A) and (C). In particular, behavior (A) reflects that their attention is more focused on the cup itself (e.g. they want to play with the cup). For instance, we observed that the infants picked up the cup and brought it to their mouth for manipulation in the early period. From 11 months old, the infants began to show behavior (B) in which they picked up (open) the cup and then looked at the location where the cup was or looked inside the cup when there was no reward on the board. This behavior suggests that the

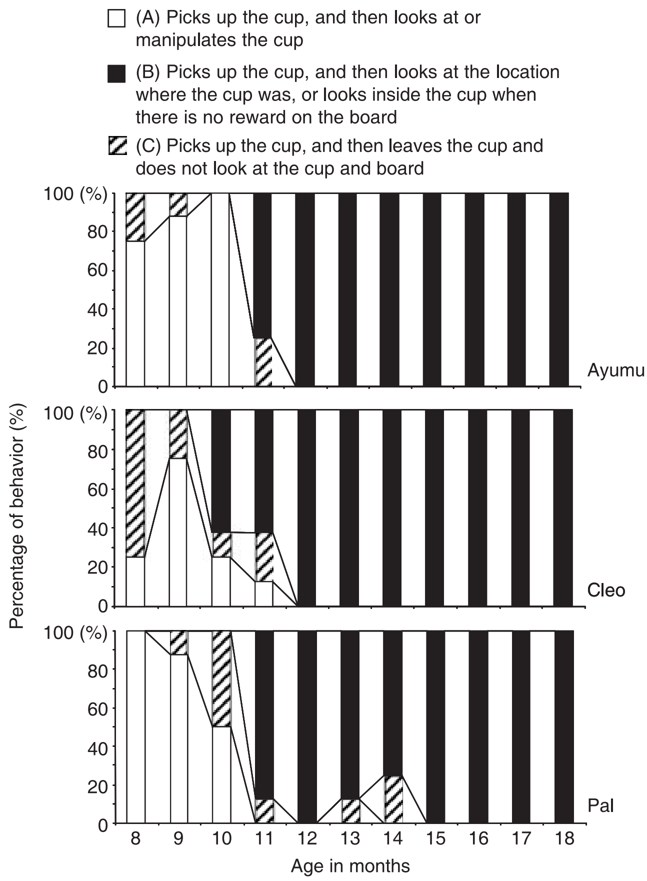

Figure 4 *The percentage of each categorized behavior as a function of the subject's age.*

subjects expected to find a reward under the cup but were not interested in the cup itself. This evidence implies that the infants were aware that a piece of reward continues to exist under one of the containers even when it is not visible. When they do not see the reward under the cup, they suspect that the reward must be hidden inside the cup. This behavioral sequence clearly shows the germination of object permanence (Piaget, 1954).

Discussion

The infant chimpanzees began to use the experimenter-given cues with increasing age. From approximately 1 year old, the infants started to use the tapping and touching cues. They started to use the pointing (close-point) cue before 2 years old. However, they showed difficulty in learning to use the gazing cues.

They could use the whole-hand pointing cue before they started to use the index finger pointing cue. There are two potential explanations for this result. First, whole-hand pointing is larger in physical appearance and therefore might be more salient compared to index finger pointing. It is very likely that more salient stimuli lead to more awareness as discriminative cues to form the association between the stimuli and objects and therefore facilitate learning. This importance of physical appearance has also been reported for human infants. Flom, Deák, Phill and Pick (2003) reported that human infants (also by 9 months) follow gaze much more reliably when it is accompanied by pointing. Pointing gestures are likely to be more salient for infants because of the movement usually involved and the better directional cueing than with head movement only (Triesch, Teuscher, Deák & Carlson, 2006). Second, captive chimpanzees typically point by extending their arm and stretching all fingers rather than by using their index finger only (Parr & Masetripieri, 2003). In contrast, index finger pointing is considered to be a stereotyped, species-typical gesture in humans. The pointing (either whole-hand or index finger pointing) is generally exhibited by primates in captivity that have been exposed to a great deal of contact with humans (Leavens & Hopkins, 1999). In other words, this gesture is not part of the natural communicative repertoire of monkeys and apes, but rather represents an adaptation to facilitate interactions with caregivers. They are less likely to point when an observer is absent or is looking away (e.g. Krause & Fouts, 1997). This gesture has been observed also in the chimpanzee community in PRI (e.g. Tomonaga, Tanaka & Matsuzawa, 2003). If the whole-hand pointing gesture is one of the 'frequent' behavioral repertoires in daily interaction with humans, it might be possible that the infants could learn to use it faster (and earlier) than the index finger pointing cue because of the daily experience within their community. In any case, the fact that the infants started to use the index finger pointing cue after they started to use the whole-hand pointing cue might be explained by stimulus generalization or the learning process facilitated by the whole-hand pointing.

Okamoto *et al.* (2002) reported the ability of an infant chimpanzee to follow experimenter-given cues in a gaze following task (the subject was Ayumu, one of the three infants in the present study). The infant started following cues with age (tapping and pointing cues: after 8 months; gazing cues: by 12 months; glancing cues: by 13 months of age). However, in the present object-choice study, the same infant showed a delayed time course in reaching criterion compared to the results from the gaze following task (tapping cues: 11 months; pointing cues: 19 months; gazing cues: 25 months of age). This infant reached criterion in the present study faster compared to the other two infants. This result could be explained by the additional exposure to experimenter-given cues in the gaze following task. If that is the case, the ability to use and not only follow the experimenter-given cues is likely to be acquired a posteriori within the object-choice task.

There are several possible reasons for this delay. First, from the analysis of the infants' behavioral changes in their pre-choice behaviors, we found that behavioral category (b), looking at the pointing cue and choosing the incorrect cup, which shows a lack of understanding of the spatial and attentional link between pointing and the cup, disappeared gradually with age until they reached criterion. At the beginning of this analysis, the infants looked at the close-pointing cue, then switched their orientation to the cup, and then sometimes chose the incorrect cup. This behavioral sequence reflects their disconnection between the pointing cue and the object. There might be a potential account from a study with human infants for this behavioral change. By the end of their first year, human infants seem to understand pointing as object-directed action and follow pointing to the referred to object (Woodward, 2005). This account might also be the case for our infant chimpanzees. They reached criterion in the close-pointing in the second year (Cleo; 16 months, Ayumu and Pal; 19 months old). Although this analysis does not specify their understanding of the referential nature of pointing, it shows clearly that they gradually developed the spatial link between the pointer (or index finger) as an agent of an object-directed action and the object.

Second, through the behavioral analysis of the infants' post-choice behaviors, we found that behavioral category (B), subject picks up the cup, and then looks at the location where the cup was, or looks inside the cup when there was no reward on the board, demonstrating a germination of object permanence (Piaget, 1954), dramatically appeared at the age of 11 months. Irrespective of the conditions of the present study, the chimpanzee infants started to reach criterion after 11 months of age. At the early stage of this experiment (at least until the subjects were 11 months old), they had not yet reached the critical cognitive milestones of object permanence. As mentioned above, previous research with human infants suggests that Piaget's (1954) search task requires infants to coordinate two separate actions (one upon the occluder and one upon the object), and young infants could fail this task because they are generally unable to perform such an action sequence (e.g. Bower, 1974; Baillargeon *et al.*, 1985). This finding from human studies suggests that our infants might already have a concept of object permanence before 11 months old. Yet, for requiring the coordinated actions, their success in the object-choice task developed with increasing physical maturity. In the present study, the subjects had experience with transparent cups through which they could see the reward on the board and under the cup before proceeding to the testing phase. Moreover, these infants made correct responses in delayed response tasks (9 months old; 1-second delay, 10–11 months old; 3-seconds delay; Okamoto, Ishii & Tomonaga, 2001). The infants should be aware and remember that a piece of food continues to exist under one of the cups even when it is not visible. As a result, in the beginning our subjects showed behavior (A), which shows only orienting to the cup itself but not to the contents of it. Then, they began to show behavioral category (B) after 11 months of age. For example, they started to grasp the cup carefully. Then, they turned it over while holding it and inspected the inside of the cup when they could not find a piece of food on the board.

As an additional point to be considered, we assume that maturity of physical posture is important in development during the early period of our experiment. The present study required the infants to approach the testing board to perform the task. To make a choice, they needed locomotion to reach the board when picking up a cup and support their body with two or three limbs. Our infants started locomotion at 5 months old by immature quadrupedalism (Okamoto-Barth, Tanaka, Kawai & Tomonaga, 2007b; Tomonaga *et al.*, 2003; cf. Doran, 1992, for a field report). However, most of the previous cognitive studies with human infants required the infants to sit on a chair to perform a task. Fontaine and Pieraut le Bonniec (1988) found that postural maturity was a better predictor of reaching than infant age in human infants. Bullinger (1990) also argued that the infant needs to develop a stable postural base for visually guided reaching. Additionally, Morange and Bloch (1996) reported that human infants under 6 months use the hand corresponding to the location of the target when reaching for it. If this is the case (at least in the early period of our experiments), the chimpanzee infants would just reach for the cup that is located on the side on which they have a free hand available while the other hand supports their posture. Although we did not investigate this assumption directly, it is likely that developing body posture and locomotion interact with performance on the task.

Itakura and Tanaka (1998) reported that human children solved this same task even with a glance-only cue (gaze without head orientation) at around 3 years of age, although they show spontaneous gaze following much earlier. However, previous research with non-human primates reports relatively poor performance in this task (but see positive results from the same community of chimpanzees by Itakura & Tanaka, 1998) even though they follow the other's gaze consistently. Gómez (2005) suggested that gaze following could be a reflex or a mechanically learned reaction and in adult chimpanzees would show a more sophisticated form. For instance, like 15-month-old human infants (Caron, Kiel, Dayton & Butler, 2002), adult or young chimpanzees and bonobos demonstrated understanding that gaze following requires an uninterrupted line of vision (Okamoto-Barth, Call & Tomasello, 2007a). However, it still remains contested whether non-human primates' gaze following is an output of some level of understanding others' mental states (Gomez, 2005 for review). Although in the present study we did not focus on understanding others' intentions *per se*, our results suggest that the use of human behavioral cues in chimpanzees develops with age and is facilitated by the development of gaze following, object permanence, and physical maturity.

In summary, our study demonstrated that infant chimpanzees begin to use experimenter-given cues with age. Moreover, the results of the detailed behavioral analysis imply that the ability to use the cues is developing and mutually related with other cognitive and physical developments. We believe that the present longitudinal study which breaks down the object-choice task into several aspects suggests new knowledge about what this task actually measures and how the infants develop the cognitive ability to solve this task. In the future, we should conduct more detailed comparative examinations concerning the developmental changes involving gazing behaviors and factors affecting performance in the object-choice task. Such studies will provide a clearer idea of visual communication including joint attention and the understanding of social-cognitive abilities in non-human primates.

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