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ORIGINAL ARTICLE

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Behavioural development in a matching-to-sample task and token use by an infant chimpanzee reared by his mother

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Abstract We investigated the behavioural and cognitive development of a captive male infant chimpanzee, Ayumu, raised by his mother, Ai. Here we report Ayumu's achievements up to the age of 2 years and 3 months, in the context of complex computer-controlled tasks. From soon after birth, Ayumu had been present during an experiment performed by his mother. The task consisted of two phases, a matching-to-sample task in which she received token rewards, and the insertion of these tokens into a vending machine to obtain food rewards. Ayumu himself received no reward or encouragement from humans for any of the actions he exhibited during the experiment. At the age of 9 months and 3 weeks, Ayumu performed his first matching-to-sample trial. At around 1 year and 3 months, he began to perform them consistently. Also during this period, he frequently stole food rewards from his mother. At 2 years and 3 months, Ayumu succeeded for the first time in inserting a token into the vending machine. Once he had succeeded in using a token, he performed both phases of the task in sequence 20 times consecutively. The infant's behaviour was not shaped by food rewards but by a strong motivation to copy his mother's behaviour. Our observations of Ayumu thus mirror the learning processes shown by wild chimpanzees.

Keywords Behavioural development · Matching to sample · Infant chimpanzees · Token use

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Introduction

Wild chimpanzees use a variety of tools, throughout all the populations from East to West Africa, and possess some inter-population differences in several patterns of behaviour (McGrew 1992; Whiten et al. 1999; Yamakoshi 2001). This variability of behaviour among wild chimpanzee populations has confirmed that humans are not the only species to exhibit culture. Cultural behaviours are transmitted through non-genetical channels. When and how are skills and knowledge passed from one generation to the next? The understanding of the mechanisms of social transmission may enhance our knowledge of the evolutionary basis of human culture.

Several previous studies have focused on the behavioural development of wild infant chimpanzees (Goodall 1986; Hiraiwa-Hasegawa 1990a, 1990b; Plooij 1984). However, there are few studies that have investigated the development of cognitively challenging skills – such as tool use in chimpanzees living in their natural habitat (Inoue-Nakamura and Matsuzawa 1997; Matsuzawa 1994, 1999). This is not surprising given the difficulty in making systematic observations on chimpanzees performing tool-use activities in the wild, and in particular, making continuous, long-term observations on the same mother–infant pair.

Data on infant development from captive studies is more abundant, but it derives mostly from studies on isolated infants reared by human caretakers, rather than by the infants' biological mothers (e.g. Hallock and Worobey 1984; Hallock et al. 1989). Therefore, studies with isolated infant chimpanzees cannot be good models of mother–infant interaction in terms of the acquisition of skills and knowledge. Social interactions between infants and other members of the community, particularly their mothers, have been suggested to be very important (Biro et al. 2003; Boesch 1991a, 1991b; Inoue-Nakamura and Matsuzawa 1997). The mother and other older members of the group act as models for the infants' behaviour. This social context did not exist in previous studies with human-reared chimpanzees, although there have been a few attempts to provide a conspecific surrogate mother (see the Washoe–Loulis pair of chimpanzees in Fouts 1997; Matata–Kanzi pair of bonobos in Savage-Rumbaugh et al. 1986).

There needs to be a relationship between studies of chimpanzee cognition carried out in the wild and those performed in the laboratory. In both cases, chimpanzees have demonstrated the ability to master cognitively challenging tasks, such as tool use in the wild and symbol use in the laboratory. In the wild, and especially concerning tool use, chimpanzee cognition is often assessed in relation to the objects that individuals use as tools, and to the complex motor patterns or actions used to reach the goal. In the laboratory, however, the subjects face a computer screen and do not have to use any objects, and the only action they have to perform is a simple touch to the screen or a simple press on the keys.

To help bridge the gap between wild and laboratory settings, the present study utilized a new task, consisting of the acquisition and use of tokens. The new system of token use (Sousa and Matsuzawa 2001) can provide an ideal situation for studying the cognitive ability of chimpanzees in the laboratory, more comparable to that in the wild. The task consisted of two steps. In the first step, the matching-to-sample phase, the chimpanzees performed a matching-to-sample task and received a token for each correct response. In the second step, the exchange-of-tokens phase, the chimpanzees had to carry the token to a vending machine, insert it, and then touch the monitor to perform a binary food choice, whereupon they received the chosen food item. Thus, this new system not only has the advantages of computer-controlled tasks, but also involves objects and complex fine-motor actions.

The task consists of a series of complex behavioural components that simulates the complexity of tool use in the wild in that several events have to be related in succession. This allows us to pinpoint when an infant begins to perform each phase of this complex behaviour. In the present study, the infant remained with his mother at all times, throughout the latter's performance of the cognitively challenging task.

Previous studies have shown that chimpanzees can use tokens in exchange for a food reward (Cowles 1937; Kelleher 1956, 1957a, 1957b, 1957c, 1958; Sousa and Matsuzawa 2001, Wolfe 1936). Tokens have been shown to be equivalent to food rewards in maintaining the subjects working in a matching-to-sample task. We have also carried out a systematic investigation on token use in adult chimpanzees including the present subject's mother (Sousa and Matsuzawa 2001).

The general goal of this investigation was to examine the behavioural and cognitive development of an infant chimpanzee. How does an infant chimpanzee acquire a cognitively challenging task? We introduced the task of obtaining and using tokens, in which an infant and his skilful mother participated in each other's presence. The specific objectives were

1. Developmental course: what is acquired by the infant and when?
2. Motivation: what is the motivation behind learning?
3. Mechanism of social transmission: what kind of interactions occur between the infant and the mother?

Methods

Subjects

A male infant chimpanzee (*Pan troglodytes*), named Ayumu, was the subject of this study (Fig. 1A). The infant was born after 235 days of gestation at the Primate Research Institute, Kyoto University on 24 April 2000. There were no complications during pregnancy, labour, or delivery. Ayumu has been successfully cared for and nursed by his mother, Ai, since birth. Ai was 23 years old at the time of delivery and had had extensive experience in computer-controlled experiments (Kawai and Matsuzawa 2000; Matsuzawa 1985a, 2001, 2003). Both infant and mother lived in a large outdoor enclosure with semi-natural conditions (Ochiai and Matsuzawa 1997), integrated in a group of 14 chimpanzees of three generations. They were cared for according to guidelines produced by the Primate Research Institute of Kyoto University and were at no time food deprived.

Apparatus

The observations were carried out in an experimental booth (approximately 180×180×180 cm) with acrylic panels as walls. The booth was equipped with computer-controlled apparatus, including two touch-sensitive screens, a vending machine, three universal feeders, and three delivery trays (see Sousa and Matsuzawa 2001). Japanese 100-yen coins were used as tokens. Food rewards consisted of pieces of apple, banana, carrot, sweet potato, blueberries, chow, grapes, peanuts, pistachios, and raisins (all approximately the same size: 1×1×1 cm, 1.2–1.5 g per piece on average).

Stimuli

The discrimination tasks used the same sets of stimuli as those in Sousa and Matsuzawa (2001): ten coloured squares (red, orange, yellow, green, blue, purple, pink, brown, white, grey); ten visual symbols called lexigrams that corresponded to the ten colours (Matsuzawa 1985b); and ten kanji (Chinese characters) that corresponded to the ten coloured squares and the ten lexigrams (Suzuki and Matsuzawa 1997).

Procedure

Mother and son were invited to enter the experimental booth from the residential outdoor enclosure. For this purpose, we simply called them by name until they spontaneously walked into the booth. During the first 4 months of Ayumu's life, he was carried into the experimental booth by Ai, but as soon as he was able to move independently, he began to walk in by himself. Both subjects were free to engage in any kind of activity inside the booth. The behaviour of the infant and his mother was continuously recorded by three video cameras [two DV cameras (SONY DCR-TRV950) and an overhead CCTV camera connected to a VHS recorder], from the beginning of the experiment until the end. Usually, each daily experiment consisted of two sessions, depending on the subjects' willingness to participate. Each session consisted of 40 trials. The experimental procedure was the same as that described in Sousa and Matsuzawa (2001) and involved two phases: a matching-to-sample phase and an exchange-of-tokens phase (Fig. 2). The distance between the vending machine in the exchange-of-tokens phase and the computer for the matching-to-sample phase was 2 m. This means that to complete the entire sequence of a trial, the sub-

Fig. 1 **A** Ayumu observing his mother performing a lexigram-to-kanji matching-to-sample trial at the age of 9 months. **B** Ayumu performing a kanji-to-colour matching-to-sample trial at the age of 2 years. He is touching the red square, which corresponds to the kanji character shown. **C** Ayumu inserting a token into the horizontal slot of the vending machine (2 years and 3 months)

ject was required to walk between the two sites corresponding to the two phases. The procedure assured that the number of token rewards (40) was constant across sessions. There was no interaction between the experimenter and the subjects during the sessions. In the period between sessions, interactions between the experimenter and the subjects – such as social play or chasing – were allowed, and the subjects also received additional food. At the end of the experiment, the subjects were invited to return to their residential outdoor enclosure.

Analysis

Data were collected through subsequent video analysis, combined with a trial-by-trial record of experimental data stored by the computer. For the purposes of analysis, we defined the start of an experimental session as the second when one of the two individuals, Ai or Ayumu, initiated the first trial by spontaneously touching an empty white circle (the "start key") displayed at the bottom of the touch screen (Fig. 2). The session ended when the 40th token was exchanged for food. With the aim of tracing developmental changes in Ayumu, we analysed the following variables in each session: attempts and successes in touching the touch-sensitive screen for the matching-to-sample phase; attempts and successes in touching the touch-sensitive screen for the exchange-of-tokens phase; attempts and successes in getting tokens; attempts and successes in getting food rewards; attempts and successes in inserting tokens; time spent near the computer for the matching-to-sample phase; and time spent near the computer for the exchange-of-tokens phase.

Results

The following sections describe, in chronological order, the development of the behavioural components of the token task in Ayumu.

The first 9 months – observing behaviour

Up to 3.5 months of age, Ayumu clung to his mother at all times, and Ai in turn embraced the baby. Ayumu watched his mother's behaviour from her breast. At the age of 4 months, Ayumu began occasionally to leave his mother's embrace, although body contact between mother and infant was observed in 68% of the time. Even in the absence of direct contact between mother and infant, Ayumu accompanied Ai as she walked back and forth between the two computers. The percentage of time spent with body contact between mother and infant decreased monotonically: 50% at the age of 4.5 months, 30% at the age of 5 months, and 6% at the age of 6 months. During the period from 6 to 9 months of age, the infant was almost completely independent of the mother. However, he never tried to touch either of the screens. Instead, he carefully observed the mother's behaviour.

Matching-to-sample phase

On 16 February 2001, when Ayumu was 9 months and 3 weeks old, he attempted for the very first time to touch the screen for the matching-to-sample task, and moreover,

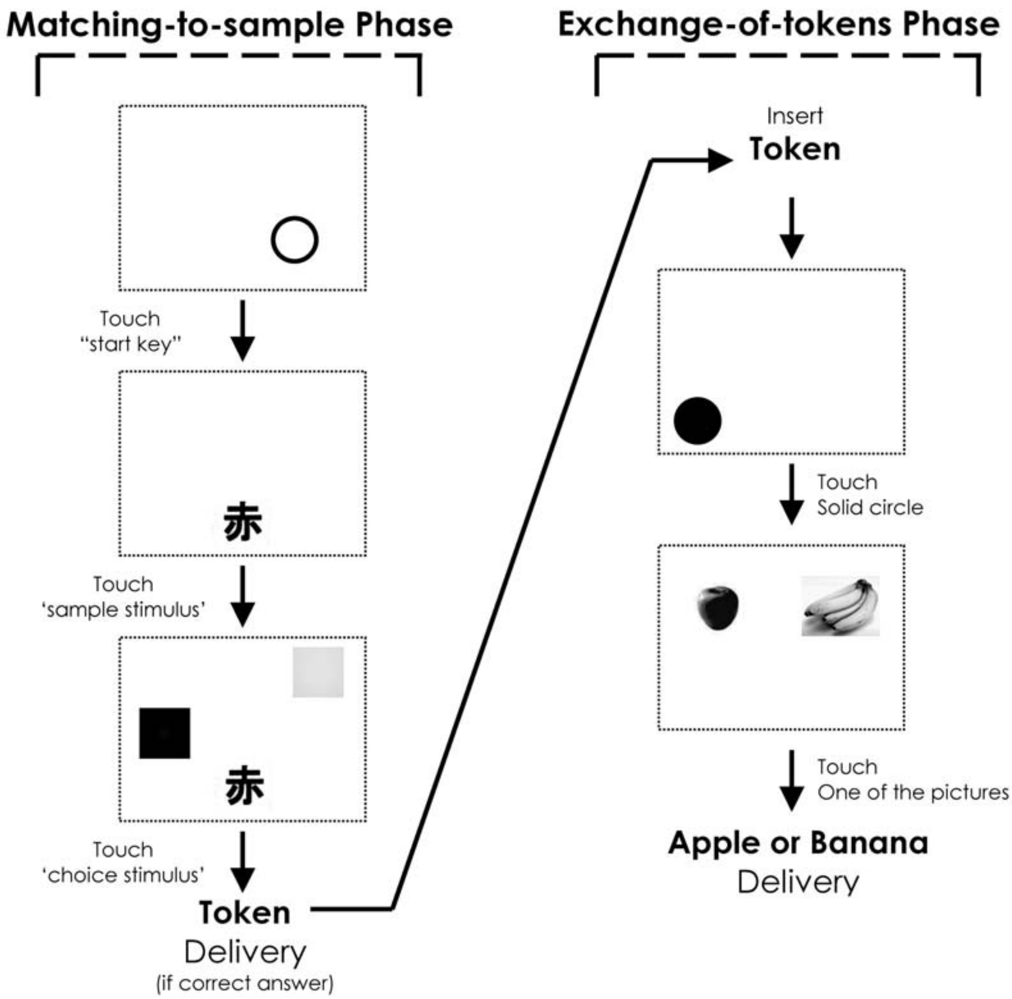

Fig. 2 Schematic diagram illustrating both phases of the token task. The *matching-to-sample phase* consisted of a matching-to-sample task with token rewards. Each trial began with the presentation of an open white circle (*open black circle* on the figure) against a black background near the bottom of the touch screen. After the chimpanzees touched this "start key", the circle disappeared and a "sample stimulus" appeared on the screen. A touch to this "sample stimulus" resulted in the appearance of two "choice stimuli" while the "sample stimulus" remained on the screen. The subject was then required to choose and touch the "choice stimulus" that corresponded to the "sample stimulus". A correct response was followed by a chime sound and the delivery of a token. An incorrect response was not rewarded and was followed by a beep sound and a "time out" of 3 s. The "start key" then re-appeared, signalling the beginning of a new trial. The *exchange-of-tokens phase* consisted of a binary food choice, using pictures presented on the screen after subjects had inserted a token into the vending machine. We prepared ten different foods as rewards. A trial began with the insertion of a token into the vending machine through a slot in the acrylic panel to the right of the touch screen. Subjects could insert as many tokens consecutively as they wished. A solid white circle (*solid black circle* on the figure) appeared on the touch screen for each token inserted. A touch to a solid white circle resulted in the appearance of pictures of two of the ten different food items used as rewards. The identity of the two food items was fixed within a session but varied between sessions. The on-screen positions of the two pictures of food items were randomised trial by trial. The subject was required to choose one of the two food items by touching the corresponding picture, which resulted in the delivery of that food item

he succeeded in completing a trial by touching three stimuli: the "start key", the "sample stimulus", and the "choice stimulus". He happened to choose the correct alternative. The matching-to-sample task used in this particular session was kanji-to-colour matching. The subject was required to choose the coloured square that corresponded to the sample kanji character. When the mother, Ai, moved to the vending machine after collecting three tokens, Ayumu, who had been observing her, approached the screen, stood upright, and touched the white circle (start key) at the bottom of the touch-screen. Following his touch, the start key disappeared and a sample stimulus appeared in the middle of the screen: the kanji character meaning "brown". He proceeded to touch this character, resulting in the appearance of two coloured squares as choice alternatives on the screen. A brown square was presented in the top-right corner of the screen, while the second alternative, a pink square, was located just beneath the brown square. Although the pink square was closer to Ayumu and the brown square was located out of his reach, Ayumu used the food tray located below the screen as a step up and stretched his body and arm until he finally touched the brown square, scoring a correct response.

After that day and up to 1 year and 3 months of age, Ayumu touched the touch-sensitive screen only sporadi-

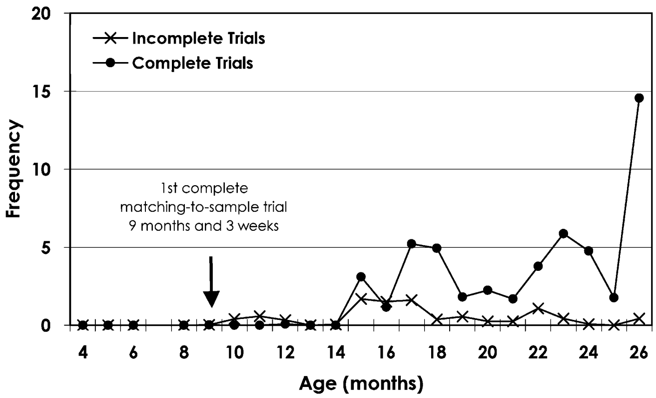

Fig. 3 Ayumu's average frequency of attempts and successes in touching the monitor for the matching-to-sample task per day for each month of age. Incomplete trials include all attempts that did not lead to a finished matching-to-sample trial, for example, attempts to touch the monitor, touching only the start key, or touching until the appearance of the sample stimulus only (see Fig. 2). Complete trials were those in which the subject performed all the necessary steps to complete a trial in its entirety

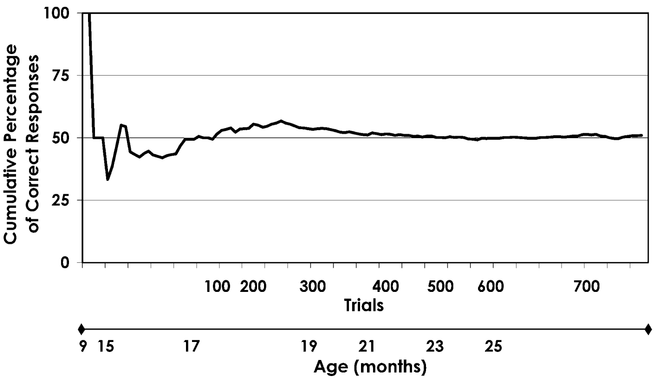

Fig. 4 Cumulative percentage of correct responses for the matching-to-sample task performed by Ayumu. Each data point indicates average accuracy per day calculated from the first day Ayumu performed a complete matching-to-sample trial until the targeted day. Only days when complete trials were performed were considered

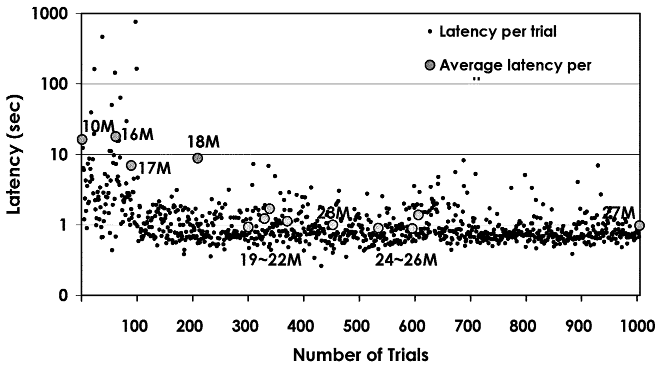

Fig. 5 Ayumu's latency to touch the choice stimulus in the matching-to-sample task, on a logarithmic scale for each complete trial. Latency is defined as the period between touching the "sample stimulus" and touching the "choice stimulus". *M* months (of age)

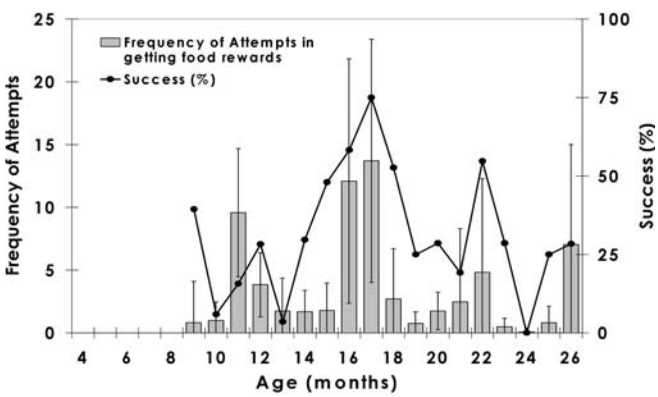

Fig. 6 Ayumu's attempts and successes in getting food rewards won by his mother, during experimental sessions at each month of age. The *bars* represent the average frequency of attempts in getting food rewards (±SD) per day (max.=80) for each month of age (*left* y-*axis*). *Black dots* represent the percentage of successes in getting food rewards per attempt at each month of age (*right* y-*axis*)

cally. However, from the age of 1 year and 3 months onwards, his attempts and actual touches to the monitor increased dramatically (see Fig. 3). The number of matching-to-sample trials (Fig. 1B) performed by Ayumu in a session was around five on average during the period from the age of 1 year and 3 months to 2 years and 2 months. Ayumu sometimes completed trials by three consecutive touches to the screen and obtained tokens when he made the correct choice. He manipulated the tokens thus received, mainly by mouthing, handling, or inserting them into the gap between the bottom of the booth door and the floor.

Figure 4 shows the cumulative percentage of correct responses scored by Ayumu from his first trial on 16 February 2001 (9 months and 3 weeks of age) onwards. Cumulative accuracy was 50%, which corresponds to chance level. This clearly demonstrates that Ayumu did not learn the symbolic relationship of the stimuli. However, his performance from the very first day showed that he did acquire the flow of behavioural components within the matching-to-sample phase. Apart from the accuracy, Ayumu's performance in the matching-to-sample phase improved steadily and came to resemble that of his mother. Figure 5 shows Ayumu's latency to touch the choice stimulus in complete trials of the matching-to-sample task. Latency was long with high variance during the first 100 trials but decreased to remain at a stable level (0.98±0.81 s on average), comparable to that shown by the mother during the same task (0.50±0.12 s on average).

Obtaining food rewards in the exchange-of-tokens phase

Close to the age of 10 months, right after his first attempt in the matching-to-sample phase, Ayumu began to attempt to steal the food rewards received by his mother at the exchange-of-tokens phase site (Fig. 6). It was only at the age of 1 year and 4 months, however, that he began persistently to steal the food rewards, increasing not only the number

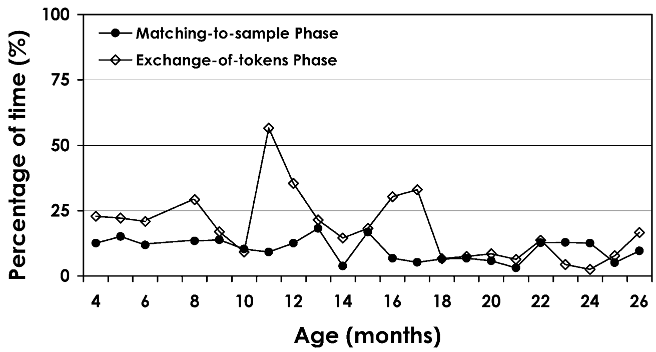

Fig. 7 Time spent by Ayumu near the computer for the matching-to-sample phase and near the computer for the exchange-of-tokens phase, at each month of age. Shown is the average of the absolute percentage of time per session at each month of age, calculated according to the time each session lasted. The infant was considered to be near a computer if he could reach either the screen or the delivery tray below it just by stretching his arm or standing up, that is, without needing to step forward

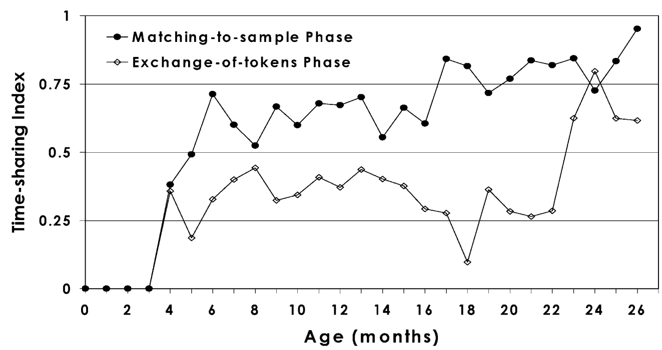

Fig. 8 Time-sharing index indicating the allocation of time between infant and mother, in both phases of the task

of attempts, but also the percentage of successes in obtaining the food. Ayumu had developed and efficient tactic, yet his attempts and successes did not increase monotonically, because the mother in turn developed a counter-tactic, precluding his access to the food she was working for. She would block Ayumu's path to the food tray with her body, or hold him at a distance with her foot. In contrast with Ayumu's efforts to steal food from his mother in the exchange-of-tokens phase, he never attempted to take tokens from her in the matching-to-sample phase.

Time allocation during the token task

For each month of age, we calculated the average percentage of time per day that Ayumu spent near the computer for the matching-to-sample phase, and near the computer for the exchange-of-tokens phase. Up to 8 months of age, time allocation was stable. Ayumu spent 13% of the time near the computer for the matching-to-sample phase and 24% of the time near the computer for the exchange-of-tokens phase on average (Fig. 7). During this period, Ayumu either was being held by his mother or accompanied her on foot as she walked back and forth between the two computers. By 11 months of age he spent more time near the computer for the exchange-of-tokens phase. This continued until 12 months of age, at which point it began to decline. Another peak was observed during the ages of 1 year and 4 months and 1 year and 5 months, after which the time spent near the computer for the exchange-of-tokens phase decreased again. These two peaks correspond to those in Fig. 6, in which Ayumu attempted to steal food as it was being delivered to the food tray.

Further analysis of time allocation revealed a time sharing of the task between infant and mother. Figure 8 shows the time-sharing index (TSI), given by the following equation: TSI=time spent alone/(time spent alone+time spent in mother's presence). This index was calculated for both phases of the token task. An index value of 1 (TSI=1) means that the infant was always alone when facing the computer, with the mother located at the other end of the booth. An index equal to 0 (TSI=0) means that Ayumu was never alone but always with his mother whenever he was facing the computer.

The results showed that Ayumu came to spend more time near the computer for the matching-to-sample phase when his mother was elsewhere in the booth. Similarly, albeit at a slightly later stage, Ayumu began to spend more time near the computer for the exchange-of-tokens phase when his mother was not there. TSIs in both phases were approaching 1. This reflects a situation in which Ayumu worked on the matching-to-sample phase while his mother worked on the exchange-of-tokens phase, and vice versa. This overall tendency demonstrates the time sharing of the task by the infant and his mother.

Attempts at token use

At 1 year and 10 months of age (23 February 2002), Ayumu attempted to insert a token into the vending machine for the first time. He used his hand, holding the token in a vertical position, although the slot he was aiming for was horizontal. He continued to try occasionally to insert tokens in the same way but never succeeded in his efforts.

Two weeks later, still at 1 year and 10 months of age (12 March 2002), Ayumu acquired another component of the exchange-of-tokens phase. Just after Ai had inserted a token, Ayumu waited in front of the food tray for the food reward. Before proceeding with the trial, Ai stood up and invited Ayumu to play, moving away from the food tray. Ayumu followed her initially, but then quickly ran back to the screen and touched the solid white circle that indicated that a token was waiting to be exchanged. His touch made the white circle disappear and two pictures of food appear on the screen. Ayumu touched one of these, receiving the corresponding food reward. This was the first time that Ayumu touched the screen in the exchange-of-tokens phase. He continued to show the same behaviour in the sessions that followed.

Token use

On 20 July 2002, Ayumu succeeded in inserting a token into the vending machine for the first time. During the first session of the day, Ayumu performed matching-to-sample trials, receiving five tokens in his first eight attempts. Suddenly, after the ninth matching-to-sample trial – which he performed correctly, receiving another token (his sixth) – he walked to the vending machine with the token in his mouth. He stood up bipedally and touched the horizontal slot with his left index finger, then climbed and inserted the token with his mouth (Fig. 1C). To reach the horizontal slot of the vending machine (84 cm above the floor) with his mouth, he had to pull his body up using the edge of the metal wall frames. After inserting the token, Ayumu climbed down and touched the solid white circle on the screen with his left index finger. This resulted in the appearance of two pictures of food on the screen. He touched the picture of a blueberry with his right index finger, received one blueberry, and ate it. This first success was followed by a series of exploratory behaviours. Ayumu climbed up to the vending machine again and touched the horizontal slot with his mouth, then with his left index finger, and then with his mouth again. It seemed as if he was "checking" the slot. Next, he went to look at the blueberries arranged on the feeder through the transparent acrylic panel, then back to the vending machine, climbing up again to touch the slot with his mouth and finger once more.

Ayumu then returned to perform more matching-to-sample trials, and whenever he received a token he rushed to the vending machine, inserted it, touched the screen, and obtained a food reward. He repeated this over and over, getting and inserting a total of 20 tokens within the same session. Meanwhile, Ai remained first lying and then sitting on the floor, watching Ayumu.

At this stage, Ayumu did not discriminate between the two pictures of different food items presented on the screen for the exchange-of-tokens phase. He exhibited a strong side bias, preferring to select the picture on the left. However, by the age of 2 years and 9 months, he began to show evidence of discrimination, choosing the picture of his favourite food regardless of its position on the screen. Table 1 summarizes Ayumu's main achievements in the token task, during the first 2 years and 3 months of his life.

Table 1 Ayumu's main achievements in the token experiment; *y* years, *m* months, *w* weeks

Age	Achievement
9 m 3 w	Performs his first matching-to-sample trial (with success)
11 m 0 w	Starts to spend more time near the food tray where food is delivered
1 y 3 m 0 w	Shows dramatic increase in attempts to touch and successes in touching the screen in the matching-to-sample task
1 y 4 m 3 w	Begins to obtain food rewards consistently, increasing not only the number of attempts, but also the percentage of successes in obtaining the food
1 y 5 m 2 w	Shows drastic decrease in attempts to obtain food rewards
1 y 10 m 0 w	Tries to insert tokens into the horizontal slot of the vending machine for the first time
1 y 10 m 2 w	Touches the screen in the exchange-of-tokens phase for the first time
2 y 3 m 0 w	Inserts token into vending machine for the first time, after obtaining it by performing a matching-to-sample trial. On the same day, he repeats the full sequence of the task 20 times consecutively

Discussion

Developmental course: what is acquired and when?

The present study has shown that at the age of 9 months and 3 weeks, an infant chimpanzee was able to perform a complete matching-to-sample trial and thus obtain a token. The infant then progressively acquired other components of the token task as well, as summarized in Table 1. At the age of 2 years and 3 months, Ayumu inserted a token into the vending machine for the first time and exchanged it for food. Hence he succeeded in completing the entire sequence of events that made up the task.

One important characteristic of Ayumu's behavioural development was the sudden and spontaneous appearance of the two main components of the task. During the first 9 months of his life, Ayumu observed his mother's behaviour from a close distance yet never made any attempt to touch either of the screens or get a reward. Then, at 9 months and 3 weeks, he suddenly performed a complete matching-to-sample trial, which involved three consecutive touches to the screen. This showed that he understood the flow of a trial. This age also coincides with the age at which orienting manipulation first appears in young chimpanzees, 8–11 months (Hayashi and Matsuzawa 2003). Ayumu, who was one of the participants of Hayashi and Matsuzawa's study, first showed object–object combination at the age of 8 months.

The ability to use tokens also appeared suddenly in Ayumu's behavioural repertoire, at the age of 2 years and 3 months. However, long before actually succeeding in inserting a token into the vending machine, he had already demonstrated an understanding of how the object was to be used: at 1 year and 10 months he made his first attempts to insert a token into the appropriate slot. This age coincides with the age at which tool-use activities first appear in chimpanzees. Hirata and Celli (2003) report that at the age of 1 year and 10 months on average, infant chimpanzees, including Ayumu, began to insert a probing tool through a small hole to obtain honey in a honey-fishing task. In the wild, it is also at this age that infants start to use tools to drink water by inserting folded leaves into a tree hole (C. Sousa and T. Matsuzawa, unpublished data).

Another important characteristic of Ayumu's development was the dramatic increase in his performance of the behaviour following the first successful attempt. In both matching-to-sample and token use, the infant drastically increased the frequency of attempts after the first successful trial. This behavioural change did not occur gradually. These results may reflect quantum jump characteristics common to cognitive development.

Intrinsic motivation to copy

When Ayumu performed his first matching-to-sample trial and was rewarded with a token, he mouthed the coin. He received not food but a piece of metal. This clearly shows that he was not motivated by food. Between Ayumu's first matching-to-sample trial (at less than 1 year old) and his first successful attempt at inserting a token into the vending machine (at more than 2 years old), 17 months had passed. During these 17 months, Ayumu received a total of 377 tokens through his matching-to-sample performance. These tokens were never exchanged for food.

The strong motivation shown by Ayumu was not food based. This fact refutes Galef's (1990) claim that social learning will not persist if food reward is not delivered. Without any food reward, Ayumu performed matching-to-sample trials. This is similar to the behaviour shown by infant chimpanzees in the wild attempting to crack open nuts (Biro et al., 2003). Chimpanzees less than 3.5 years old never succeed in cracking open nuts. This means that they never receive any food reward as a direct result of their own efforts, yet they do eventually succeed in developing the skill. They must therefore be driven by a strong and intrinsic motivation to produce a copy of the adults' behaviour.

Mechanism of social transmission

Although the environment in which the present experiment was conducted was artificially created by humans, no humans were directly involved in Ayumu's learning process. In other words, the infant's behaviour was not positively or negatively reinforced by the experimenter or any other person at any point during the study. The infant chimpanzee acquired the entire process from his mother. Video records of the mother's behaviour revealed that she was not actively involved in the learning process of her son. She did not show any moulding or other form of teaching. In the wild, there have been two reported episodes of active teaching performed by chimpanzees, both performed by mothers as their infants were learning to crack nuts in the Taï Forest (Boesch 1991b). However, it must be noted that these episodes were the only two ever recorded over many years of observation at the site. Among the Bossou community of chimpanzees, about 200 km away from the Taï Forest, no teaching has been observed throughout more than two decades of study (Biro et al. 2003).

Although the chimpanzee mother in our study did not exhibit any teaching-like behaviour, she did show high levels of tolerance towards her son's behaviour. Ai always allowed Ayumu to move freely inside the experimental booth and to touch any of the apparatus she was using. She also tolerated her son's behaviour of stealing food rewards up to a certain limit. Her behaviour was thus much more strongly reminiscent of wild chimpanzee mothers' whose infants are in the process of learning a tool-using behaviour (Matsuzawa et al. 2001).

In spite of the imitative abilities of chimpanzees being far from those of humans (Nagell et al. 1993), the infant did copy his mother's behaviour. An important point to bear in mind is that our study was carried out without separating the infant from the mother. The model for the infant's behaviour was therefore his own mother, rather than an individual of another species. This is in contrast with many previous studies of imitation in which humans served as behavioural models (e.g. Nagell et al. 1993). In the majority of experiments in captivity concerning the mechanisms of social transmission, the models were not conspecifics and the tests were based on single trials, which explains why these experiments have occasionally failed (de Waal 2003). In the mimetic process of chimpanzees the models should be conspecifics and the learning process should be based on long-term observation of the target behaviour. This may also shed some light on the case of bonobos (*Pan paniscus*), who spontaneously learned associations between symbols and objects, in contrast with chimpanzees (*Pan troglodytes*), who failed (Savage-Rumbaugh et al. 1986). It is not necessary to invoke a species difference to explain this result. The bonobos had access to their mothers, whom they could observe using symbols, whereas the chimpanzees were raised by humans and had no experience with conspecific models.

Overall, the learning process through which Ayumu acquired new skills during this study was characterized by close observation of the mother by the infant for extended periods of time, spontaneity, strong and intrinsic motivation for making a copy of the behaviour, and high levels of tolerance from the mother. These features are similar to those evident in learning processes in wild chimpanzees, referred to as 'education by master-apprenticeship' (Matsuzawa et al. 2001), or BIOL (bonding- and identification-based observational learning, de Waal 2001).

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