



Brief article

Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*)

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Abstract

We studied gaze perception in three infant chimpanzees (*Pan troglodytes*), aged 10–32 weeks, using a two-choice preferential-looking paradigm. The infants were presented with two photographs of a human face: (a) with the eyes open or closed, and (b) with a direct or an averted gaze. We found that the chimpanzees preferred looking at the direct-gaze face. However, in the context of scrambled faces, the infants showed no difference in gaze discrimination between direct and averted gazes. These findings suggest that gaze perception by chimpanzees may be influenced by the surrounding facial context. The relationship between gaze perception, face processing, and the adaptive significance of gaze perception are discussed from an evolutionary perspective.

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1. Introduction

Among facial features, the eyes are a significant area of focus for animals. Following the gaze of others can help individuals perceive the location of important components of the environment, such as food and predators, and can facilitate certain kinds of social interaction among group mates (Langton, Watt, & Bruce, 2000; Tomasello, Call, & Hare, 1998). The rapid detection of the eyes of another organism should therefore have considerable adaptive significance.

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From an evolutionary viewpoint, several researchers have suggested that animals may have a specialized neural system within the brain that is devoted to gaze processing (Baron-Cohen, 1995; Langton et al., 2000; Perret & Emery, 1994; Perret, Hietanen, Oram, & Benson, 1985).

There is evidence from a developmental perspective to support these claims. Human infants are very sensitive in their perception of eyes and eye-like stimuli. Some developmental studies of gaze discrimination have indicated that the ability to discriminate gaze direction may emerge when infants are between 3 and 4 months old. Samuels (1985), for example, presented 3-month-old infants with two faces that were identical, except that one had a direct gaze and the other an averted gaze; the infants did not discriminate between the two. By the time infants are 4 months old, however, they are able to discriminate between direct and averted gazes (Farroni, Johnson, Brockbank, & Simion, 2000; Vecera & Johnson, 1995).

This raises the question of whether the ability to detect gaze is ‘hardwired’. Two hypotheses have been proposed regarding the onset of this ability. One is that eye-direction processing is the product of an ‘encapsulated’ module that is present from birth (Baron-Cohen, 1994, 1995). Batki, Baron-Cohen, Wheelwright, Connellan, and Ahluwalia (2000) demonstrated that neonates younger than 2 days old looked longer at a photo of a face with the eyes open than they did at a photo of the same face with the eyes closed.

The second hypothesis suggests that this ability develops over the first few months of life (Farroni et al., 2000; Vecera & Johnson, 1995). Vecera and Johnson (1995) revealed that infants did not discriminate gaze any more efficiently when intact eyes were presented in the context of a scrambled face than they did when the eyes were presented within an intact face, suggesting that gaze information is not completely isolated from facial information, in contrast with the modular hypothesis.

The view that there is a developmental change in processing gaze direction is an extension of the structural hypothesis claimed by Johnson and colleagues. Johnson, Dziurawiec, Ellis, and Morton (1991) demonstrated that newborns, only minutes old, can track an intact schematic face better than a scrambled schematic face. Johnson (1990) proposed that a subcortical visual pathway involving the superior colliculus controls preferential orienting towards face-like stimuli in the first month after birth. Johnson and Morton (1991) applied the term “Conspec” to this primary mechanism. Conspec operates from the moment of birth, but its functioning rapidly declines after 1 month. A second mechanism, named “Conlern”, was thought to be acquired around 2 months of age. Johnson and Morton (1991) proposed that there was a developmental shift in processing from the subcortical visual pathway to the second mechanism that appears in plastic cortical visual pathways. This mechanism is thought to acquire information associated with faces, including facial expressions, identities, and the direction of gaze, through each individual’s experience of faces.

This controversy concerning the development of gaze discrimination in humans raises a question about the phylogenetic origin of gaze perception. If non-human animals also possess a neural mechanism dedicated to gaze processing, then a case can be made for the adaptive benefits of gaze perception.

The developmental time course of gaze perception in non-human animals must also be

considered. Maturation of the neural substrate for gaze processing may differ between humans and non-human animals. Developmental studies of gaze discrimination in non-human animals can help us to understand the postnatal maturation of species-specific brain activity underlying this ability.

Chimpanzees (*Pan troglodytes*), our closest evolutionary relatives, have much in common with humans, especially during the early stages of life. Recent comparative studies suggest that there are similarities between the early competence of human and chimpanzee neonates when they are measured with the same cognitive tests (Bard, Platzman, Lester, & Suomi, 1992; Myowa, 1996; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003).

In this paper, we examined the gaze sensitivity of infant chimpanzees from both phylogenetic and ontogenetic perspectives. First, we investigated their ability to discriminate between (a) open and closed eyes, and (b) direct and averted gazes. In addition, we investigated whether gaze sensitivity was influenced by the surrounding facial context. We presented the chimpanzees with intact and scrambled faces that showed either a direct or an averted gaze. If facial configuration is important in gaze discrimination, then the infants should be more efficient in discriminating direct from averted gazes in intact faces than in scrambled faces. On the other hand, if the gaze module hypothesis is correct, the infants should show no difference in gaze discrimination between the two facial contexts.

2. Method

2.1. Subjects

Three infant chimpanzees participated in the experiment: a male, named Ayumu, and two females, named Cleo and Pal (see Fig. 2). They had been reared with their biological mothers since birth in the Primate Research Institute, Kyoto University, and lived in an outdoor compound with eight adult chimpanzees. Ayumu and Pal were conceived by artificial insemination. These infants had been used as subjects for a research project on chimpanzee development, and had therefore experienced a variety of tests related to the development of cognitive abilities (Matsuzawa, 2001). Their mothers had also participated in cognitive experiments (Kawai & Matsuzawa, 2000; Matsuzawa, 1985; Myowa-Yamakoshi & Matsuzawa, 1999, 2000; Tanaka, 1996; Tomonaga, 1998). Care and use of the chimpanzees adhered to the *Guide for the Care and Use of Laboratory Primates* (1986) of the Primate Research Institute, Kyoto University.

2.2. Stimuli

The stimuli consisted of color photographs of a graduate student in our laboratory, a female with dark brown eyes. We created six conditions (Fig. 1). We investigated the infant chimpanzees' ability to discriminate gaze from the following three perspectives. First, we investigated their ability to discriminate between faces with open and closed eyes, and between faces with direct and averted gazes (Conditions 1 and 2). Second, we set

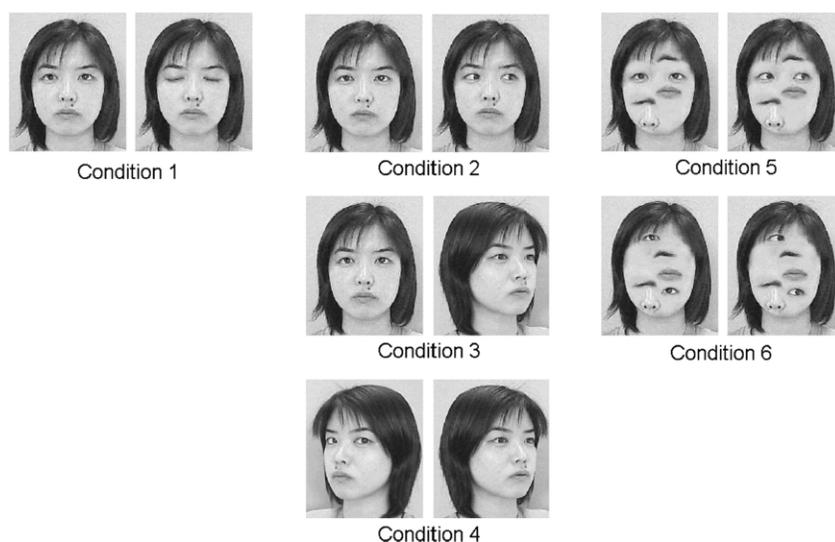


Fig. 1. The ten photographs used in the experiment.

the head in different directions, to explore the influence of face orientation on their ability to discriminate between direct and averted gazes (Conditions 3 and 4). Third, Conditions 5 and 6 were aimed at investigating the ability to discriminate between directed and averted gaze in scrambled faces, where the position of the eyes was either intact or scrambled.

Condition 1: *Open* (Frontal view) vs. *Closed* (Frontal view)

Condition 2: *Direct* (Frontal view) vs. *Averted* (Frontal view)

Condition 3: *Direct* (Frontal view) vs. *Averted* (3/4 view)

Condition 4: *Direct* (3/4 view) vs. *Averted* (3/4 view)

Condition 5: *Direct* (Frontal view, scrambled with intact eyes) vs. *Averted* (Frontal view, scrambled with intact eyes)

Condition 6: *Direct* (Frontal view, all features scrambled) vs. *Averted* (Frontal view, all features scrambled)

A total of ten photographs were used in the experiment (Fig. 1). They were taken with a digital camera (Olympus, model C-990 Zoom) and retouched using several software packages (Jasc Software, Inc., PaintShop Pro, and Adobe Systems, Inc., PhotoShop) before being printed out with a laser color printer (Seiko Epson Corp., model LP-8200C). The photographs were then enlarged to 18.0 × 15.0 cm and mounted on posterboard. The faces were cropped such that they occupied most of the photograph. The eyes were approximately 0.5 cm high and 1.2 cm wide.

2.3. Procedure

To assess developmental changes in gaze perception, the chimpanzees were tested once every few weeks between 10 and 32 weeks of age (Ayumu: 25–32 weeks, Cleo: 16–27

weeks, Pal: 10–31 weeks). Each infant was subjected to eight sessions during the testing period.

We have been carrying out the cognitive tests of infant chimpanzees reared by their mothers living in a community in the enriched environment (Ochiai & Matsuzawa, 1997). We invited the mother–infant pair to an experimental booth, then a human tester sat face-to-face with an infant. A two-choice preferential-looking paradigm was used (cf. Myowa-Yamakoshi & Tomonaga, 2001a,b). The infant was shown two photographs. A single trial involved presenting the infant with two faces, placed 30 cm apart, one to the left and one to the right. The left–right positions of the faces were randomly alternated from trial to trial, and the order of presentation in each trial was randomly selected each day. The tester presented the faces approximately 25 cm from the infant’s face. One session consisted of 12 trials, and each infant took part in one session per day. Ayumu and Pal participated in a total of 96 trials under Conditions 1–6. Cleo was unable to complete the entire set of trials under Conditions 5 and 6; thus, she took part in a total of 64 trials under Conditions 1–4.

A trial started when an infant spontaneously looked at the stimulus. During each trial, the researcher continued to present the infant with the stimulus, irrespective of the duration of fixation. A trial lasted for 15 s after the stimulus had been presented. During the trial, the infant’s responses were videotaped using a small CCD camera (Sony, model CCD-MC100) attached to the middle part of the stimulus (Fig. 2).

2.4. Data analysis

The videotapes were later examined to determine (a) which face the infant looked at, and (b) how long the infant looked at the face. Two judges scored the infant’s response (looking left, right, or elsewhere) independently, every ten frames (0.33 s interval). To calculate the reliability of the data, one judge checked all trials, while the other judge, who was blind to both the purpose of the study and to which stimulus the infant was actually looking at, scored 10–12% of the total trials for each infant. Reliability between the two judges was sufficiently high (Cohen’s kappa, Ayumu: 0.72, Cleo: 0.78, Pal: 0.87). On the basis of the coded data, we then calculated the time that each infant spent looking at each of the photographs.

Because the sample size was small in this study, we analyzed the data for each infant respectively. For each session, the mean time spent looking at the photographs was

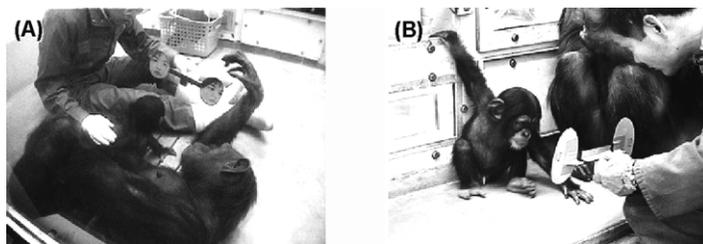


Fig. 2. Experimental situations of (A) Pal and (B) Ayumu. The infant, facing the human tester, was shown two face photographs. A small CCD camera was attached onto the middle part of the stimulus. The infant’s performance was recorded.

calculated under each condition. The mean times were 3.30 s (SD = 1.78) for Ayumu, 3.74 s (SD = 2.43) for Cleo, and 4.32 s (SD = 2.71) for Pal. Since the looking time data for each subject were not normally distributed, we logarithmically transformed the data for statistical analyses. The figure presented in this paper is based on untransformed data. For each condition for each subject, we conducted paired-comparison *t*-tests between the mean looking time data for direct-gaze (open-eyes) and averted-gaze (closed-eyes) faces separately. Thus, we did not make statistical comparisons among conditions.

3. Results

3.1. Developmental changes in gaze perception

To detect developmental changes, we initially calculated a preference score as the proportion of time spent looking at the direct gaze as opposed to the total time spent looking at direct and averted (closed) gaze stimuli. We calculated Pearson's correlation coefficients between these preference scores and age at testing (in days) for each condition. We also obtained correlation coefficients between total looking time and age for each condition. We found a significant increasing trend in preference scores as a function of age only under Condition 2 for Ayumu ($r = 0.94$, $t[6] = 6.89$, $P < 0.001$, see Appendix A). With this exception, we found no consistent developmental changes in the gaze perception of the infants; age seemed to have little effect on the chimpanzees' perception of gaze during the testing periods. We therefore did not treat the age factor in our analysis of the following data for each infant under each condition (i.e. we did not compare data by age classes).

3.2. Sensitivity of gaze perception under each condition

The mean times that each infant spent looking at the stimuli under each condition (plus the standard error of the mean) are shown in Fig. 3. We applied paired *t*-tests to the following results.

Under Conditions 1–4, we found significant differences between the two faces: under Condition 1, the infants looked longer at the frontal face with the eyes open than at the frontal face with the eyes closed (Ayumu: $t[7] = 2.63$, $P = 0.050$; Cleo: $t[7] = 2.57$, $P < 0.05$; Pal: $t[7] = 2.95$, $P < 0.05$). Under Conditions 2–4, the infants looked longer at the faces with the direct gaze than at the faces with the averted gaze, irrespective of face angle (i.e. frontal or 3/4 view: Condition 2, Ayumu: $t[7] = 3.49$, $P = 0.01$; Cleo: $t[7] = 6.51$, $P < 0.001$; Pal: $t[7] = 6.22$, $P < 0.001$; Condition 3, Ayumu: $t[7] = 2.36$, $P = 0.05$; Cleo: $t[7] = 2.77$, $P < 0.05$; Pal: $t[7] = 4.25$, $P < 0.01$; Condition 4, Ayumu: $t[7] = 2.25$, $P = 0.059$; Cleo: $t[7] = 5.44$, $P < 0.001$; Pal: $t[7] = 2.44$, $P < 0.05$).

On the other hand, under Conditions 5 and 6, there were no significant differences between the two faces. The infants did not look differently at the scrambled faces with direct and averted gazes (Condition 5, Ayumu: $t[7] = 0.87$, n.s.; Pal: $t[7] = 0.42$, n.s.; Condition 6, Ayumu: $t[7] = 0.13$, n.s.; Pal: $t[7] = 1.25$, n.s.).

The data for the youngest infant among the three were those for Pal at 10 weeks old. In her first session, she looked at the direct-gaze faces for 6.17 s (SEM = 1.57) and at the

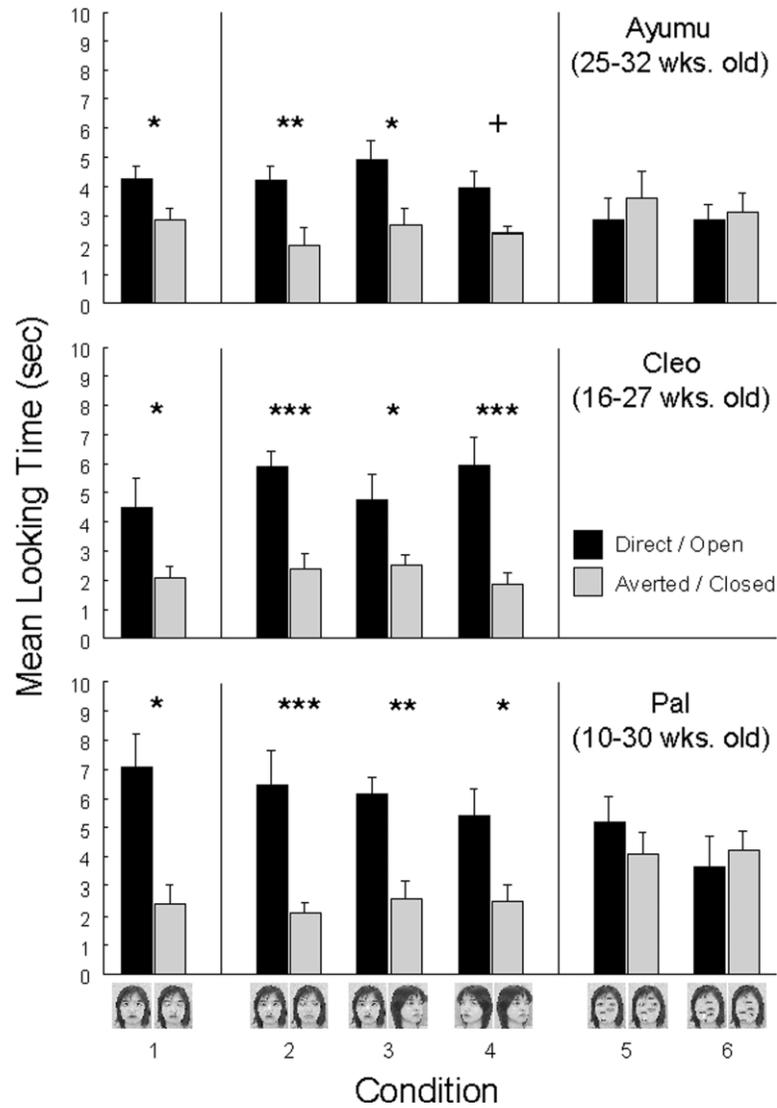


Fig. 3. The mean looking times to the stimuli in each condition for each infant (plus standard error of mean).

averted-gaze/closed-eyes faces for 1.96 s (SEM = 0.58), averaged across trials for Conditions 1–4 ($t[7] = 3.02, P < 0.05$, using log-transformed data). This suggests that at 10 weeks of age, she was already able to discriminate gaze direction.

4. Discussion

We demonstrated that infant chimpanzees, aged 10–32 weeks, preferred looking at

faces with the eyes open than at faces with the eyes closed. We also found that they preferred looking at faces with a direct gaze than at faces with an averted gaze.

These results suggest that infant chimpanzees pay attention to the gaze of other organisms. Humans are therefore not unique among primates in their ability, shortly after birth, to perceive the eyes of another organism and the direction in which they are gazing.

However, we still do not know whether the ability to perceive gaze is present at birth in chimpanzees. When we began this study, our chimpanzees had already passed the neonatal stage (Goodall, 1986). Although there is room for argument regarding the existence of an innate ‘gaze’ module in neonates, our results have implications for the development of gaze perception. Gaze perception by the chimpanzees did not generally change during the testing periods. When Pal was 10 weeks old, she was already able to discriminate gaze direction. These results suggest that, by the age of 10 weeks, chimpanzees have developed the ability to perceive gaze.

There is another important issue regarding the existence of a gaze module. In the context of scrambled faces, the chimpanzees did not look differently at the faces with direct and averted gazes. This finding is consistent with the hypothesis proposed by Vecera and Johnson (1995) that gaze perception may depend upon prolonged exposure to faces during the first few months of life. Our results do not support the specialized gaze module theory that has been claimed for humans. However, there is still the possibility that the chimpanzees did not regard the scrambled faces as “faces” but as attractive stimuli. For this reason, the chimpanzees might have paid attention to the scrambled faces, irrespective of eye-gaze direction. To confirm this point, additional studies are needed to investigate chimpanzees’ sensitivity to the facial features as early as possible after birth. For example, we might go on to compare stimuli containing only eyes with those containing no eye stimuli (i.e. containing the other facial features such as mouth and nose).

Comparative cognitive research studies have revealed that non-human primates have evolved accurate perception of the direction of eye-gaze (Emery, Lorincz, Perret, Oram, & Baker, 1997; Lorincz, Baker, & Perret, 1999; Tomasello et al., 1998). For example, Mendelson, Haith, and Goldman-Rakic (1982) showed that rhesus monkeys (*Macaca mulatta*) begin to avoid conspecifics’ gaze by the age of 3 weeks. The monkeys inspected conspecifics’ faces, looking back at them less than they looked at them when the conspecifics’ faces were looking away.

However, in examining the nature of gaze processing from the perspective of the developmental process, especially the early developmental process, our recent work is beginning to indicate that there may be species differences in non-human primates. Myowa-Yamakoshi and Tomonaga (2001a) tested a lesser ape, the infant gibbon (*Hylobates agilis*) from 1 to 6 weeks of age. During the experimental period, the gibbon’s sensitivity to gaze direction was not influenced consistently by facial context. The gibbon was able to discriminate gaze direction perfectly in both scrambled and inverted faces, as well as in upright faces, whereas in our study, the gaze perception of chimpanzees was influenced by the surrounding facial context, as is the case in human infants.

Of course, we cannot deny the possibility that, similar to the gibbon, the chimpanzees’ gaze processing prior to 10 weeks of age was independent of facial context. On the other hand, it is also possible that the gibbon infant showed gaze processing that was dependent on facial context after the experimental period ended at 7 weeks of age. Ferrari, Kohler,

Fogassi, and Gallese (2000) examined the ability to follow gaze in juvenile (age 2–6 years) and adult (age over 6 years) pig-tailed macaques (*Macaca nemestrina*). Their results showed that gaze following was more frequent in adults than in juveniles. This study suggests that in monkeys this ability may show a gradual developmental change over several years of life, from relatively young ages.

Future research based on longitudinal observation is needed to confirm whether there are differences between species in the developmental process of gaze processing across a wider variety of non-human primates. Here, we are able to stress only that, in great apes at least, general facial information has a strong effect on processing gaze from very shortly after birth. This implies that facial information plays a significant role in survival during infancy.

In great apes, gaze perception seems to be an important mother–infant communicative skill that has adaptive benefits. From birth, humans engage in the face-to-face mode with their mothers. Chimpanzees, both in the wild and in captivity, also engage in face-to-face interactions with mutual gazing during their first 3 months of life (Bard, 1994; Bard, Myowa-Yamakoshi, Quinn, Tomonaga, & Matsuzawa, 2002; Plooij, 1984). For survival, it may be crucial for infants to perceive gaze early, as it may help to attract the attention of caretakers and increase the opportunities for receiving care (Myowa-Yamakoshi, 2001).

Chimpanzees use various facial expressions, such as the play-face, in their communication (de Waal, 1982; Goodall, 1986). Chimpanzee neonates can imitate several facial gestures, by attending to the oral area (Bard & Russell, 1999; Myowa, 1996; Myowa-Yamakoshi et al., 2003). Moreover, chimpanzees seem to recognize their mothers' faces in face-to-face communication by the time they are 1 month old. We previously tested developmental changes among the three infant chimpanzees in their preference for their mothers' faces, and the results showed that after 4 weeks of age the infants began to show a strong preference for their mothers' faces (Tomonaga, Okamoto, Myowa-Yamakoshi, & Yamaguchi, 2002).

We assume that facial information, not only gazing but also facial expression, is used for mother–infant communication. Consequently, facial configuration in great apes has influenced the ability to perceive gaze, and gaze processing has not been completely isolated from facial information processing. In the present study, we used the human face as the testing stimuli. To verify this hypothesis, further research is needed to confirm whether chimpanzee infants can also discriminate gaze direction when viewing faces of their own species.

In conclusion, gaze perception in great apes, including humans, may not be simply a product of an innate module that is automatically processed. Rather, this ability may depend upon prolonged exposure to faces and may develop during the first few months of life. Few experimental studies have investigated early cognitive development in non-human primates. A phylogenetic comparison of early cognitive ability in a greater diversity of species will help us to understand the relationship between gaze perception, face recognition, and mother–infant communication.

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Appendix A. Pearson's correlation coefficients between the preference scores and age, and the correlation coefficients between total looking time and age (LT), for each condition

		Condition						All trials
		1 Open/ Close	2 Direct/ Averted	3 Direct/ Averted	4 Direct/ Averted	5 Direct/ Averted	6 Direct/ Averted	
	Ayumu	0.94	−0.05	0.36	0.17	0.25	−0.20	
	Cleo	0.04	−0.57	−0.04	0.03			
	Pal	−0.04	0.22	−0.13	−0.08	−0.30	−0.18	
LT	Ayumu	−0.31	−0.39	−0.38	0.40	−0.35	−0.54	−0.54
	Cleo	−0.29	−0.52	−0.25	−0.59			−0.52
	Pal	−0.45	−0.31	0.63	0.11	−0.59	−0.34	−0.37

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