

Spider Monkeys (*Ateles geoffroyi*) and Capuchin Monkeys (*Cebus apella*) Follow Gaze Around Barriers: Evidence for Perspective Taking?

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Gaze following is an adaptive skill that might have been selected in social species, such as many nonhuman primates, to obtain information about food location, predators, and social interactions. The authors investigated the ability of spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*) to follow the gaze of a human around barriers and the presence of “looking back” behavior. In the 1st experiment, a human looked to a target location inside the testing room, whereas in the 2nd experiment, the human looked behind an opaque barrier placed outside the testing room. The authors compared the frequency of looking at the target location with the corresponding baseline looking frequencies. Both species (a) showed evidence of spontaneous gaze following in the 1st experiment and (b) engaged in gaze following behind the barrier in the 2nd experiment. In contrast, neither species performed “looking back” responses. The authors conclude that both monkey species showed some indication of perspective-taking abilities, although the absence of “looking back” behavior suggests a potential difference from the abilities shown by the great apes.

Keywords: gaze following, spider monkeys, capuchin monkeys, comparative cognition

Gaze following, defined as “looking where someone else is looking” (Butterworth & Jarrett, 1991), is an adaptive skill that might have been selected as a means to obtain information about

food location, predators, and social interactions among group members (Tomasello, Call, & Hare, 1998). Gaze following to distant locations has been reported in a variety of animals, including dogs (Miklosi, Polgardi, Topal, & Csanyi, 1998), goats (Kaminski, Riedel, Call, & Tomasello, 2005), and ravens (Bugnyar, Stoewe, & Heinrich, 2004), but most of the evidence comes from studies on primates (e.g., Braeuer, Call, & Tomasello, 2005; Itakura, 1996; Tomasello et al., 1998). The cognitive underpinnings of this behavior have received considerable research attention. Following a distinction used to differentiate the first stages in the development of human children’s gaze following, Povinelli and Eddy (1996b) distinguished a low-level from a high-level explanation of animals’ gaze-following behavior. According to the low-level or orienting-response explanation, animals’ gaze following would be nothing but an innate response triggered by something shifting their attention (like a human’s head turn) to an external target. The presence of external visible targets would in turn reinforce this gaze-following behavior through time (Corkum & Moore, 1998). According to the high-level or perspective-taking explanation, instead, animals’ gaze following would also imply an understanding of what others see. Like human children, animals would develop an endogenous voluntary shift of attention, understanding others’ perceptions, and relying on their own expectancies and intentions (Corkum & Moore, 1998). Through time and experience, they would become able to intentionally and attentionally gaze follow potential targets and to understand the intentional referential nature of looking, the mentalistic experience of seeing, and the role of the eyes (Brooks & Meltzoff, 2002; Butterworth & Jarrett, 1991).

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There is considerable evidence supporting the high-level explanation in the great apes. Povinelli and Eddy (1996a) found that chimpanzees could follow an experimenter's gaze moving around opaque barriers to locate a hidden target. Tomasello, Hare, and Agnetta (1999) confirmed this result and additionally showed that chimpanzees were capable of ignoring distracting objects that they encountered while turning to look in the direction indicated by the experimenter's gaze. Moreover, Call, Hare, and Tomasello (1998) found that chimpanzees followed human gaze, and even looked back to the human's face when they did not find anything interesting in the target location. This "looking back" behavior is considered evidence that the performer has expectancies and understands that gaze is about something specific in the environment (Butterworth & Cochran, 1980). According to Tomasello et al. (1999), the above results show that chimpanzees understand that other individuals can see different things, thus taking a perspective different from their own. Braeuer et al. (2005) found that all great apes engaged in "looking back" behavior and gaze following behind barriers, thus extending the perspective-taking explanation to all great apes. Itakura (1996) and Povinelli and Eddy (1996a) also found that chimpanzees and one orangutan could follow the experimenter's gaze when the experimenter moved the eyes but not the head, and Tomasello, Hare, Lehmann, and Call (2007) found that chimpanzees, bonobos, and gorillas used both head and eye direction in gaze following, although head direction was more important than eye direction. Finally, chimpanzees (and macaques) show a developmental progression in gaze-following response, which is comparable to the earliest stages of human children, with adults being able to use this skill in a more flexible way (Ferrari, Kohler, Fogassi, & Gallese, 2000; Okamoto et al., 2002; Tomasello, Hare, & Fogleman, 2001).

In the first study on monkey gaze following, Itakura (1996) failed to find evidence of gaze following in capuchin monkeys, squirrel monkeys, and macaques. Other studies, however, have convincingly shown that sooty mangabeys, macaques, Diana monkeys, and one gibbon spontaneously follow the gaze of conspecifics (Emery, Lorinez, Perrett, Oran, & Baker, 1997; Scerif, Gomez, & Byrne, 2004; Tomasello et al., 1998) and humans (Anderson & Mitchell, 1999; Inoue, Inoue, & Itakura, 2004; Tomasello et al., 2001). Several findings seem to support the idea that monkeys may also possess the neural mechanisms necessary for detecting gaze direction and head orientation (Perrett et al., 1985). Recently, ring-tailed lemurs have also been reported to follow conspecifics' gaze (Shepherd & Platt, 2008), although previous studies have found no such evidence for following an experimenter's gaze in other lemur species (Anderson & Mitchell, 1999; Itakura, 1996). Although the evidence for monkey gaze following to distant locations is strong, the evidence supporting the high-level interpretation is quite fragmentary, especially when it comes to gaze following around barriers and "looking back" behavior. Marmosets can follow a human's gaze past distractors, but they do not follow the gaze around barriers (Burkart & Heschl, 2006, 2007), whereas long-tailed macaques show "looking back" behavior (Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008).

To summarize, the evidence for the perspective-taking explanation of gaze following in the great apes seems no longer controversial, whereas it is so in monkeys. There are two reasons for this. First, the information about gaze following around barriers and "looking back" behavior is scarce, making it hard to interpret

monkeys' gaze following in terms of high- or low-level explanations. Second, most of the evidence for gaze following in monkeys is based on studies on Old World species, whereas there is very little information about gaze following in New World monkeys, especially those living in complex social systems. The goal of this study was to fill this gap in our knowledge. We followed the procedure of Braeuer et al. (2005) to test gaze following to distant locations and around barriers and "looking back" behavior in spider monkeys and capuchin monkeys. Using their procedure allowed us to directly compare our results with those available for the great apes. This comparison is particularly interesting because both spider monkeys and capuchin monkeys belong to the family Cebidae and live in complex social systems (Aureli & Schaffner, 2008; Fragaszy, Visalberghi, & Fedigan, 2004). We hypothesized that social complexity might be a good predictor of gaze-following behavior in monkeys (Tomasello et al., 1998), despite the fact that the study species do not share a recent common ancestor with the great apes.

Method

Subjects

We tested 13 spider monkeys (*Ateles geoffroyi*) housed at the Centenario Zoo in Merida, Mexico, and 12 capuchin monkeys (*Cebus apella*) housed in the Institute of Cognitive Sciences and Technologies-CNR Primate Centre in Rome, Italy. The subjects were sexually mature individuals of both sexes and of various ages (see Table 1). Both species were housed in social groups in

Table 1
Species, Age, and Sex of Subjects

Subject	Age	Sex
Spider monkeys		
1	Subadult	Female
2	Subadult	Female
3	Subadult	Male
4	Subadult	Male
8	Adult	Female
9	Adult	Female
11	Adult	Female
21	Adult	Male
22	Adult	Male
23	Adult	Male
24	Subadult	Female
31	Adult	Female
32	Adult	Female
Capuchin monkeys		
Robin Hood	Adult	Male
Rubens	Subadult	Male
Cognac	Adult	Male
Pedro	Subadult	Male
Roberta	Adult	Female
Sandokan	Subadult	Male
Penelope	Subadult	Female
Vispo	Subadult	Male
Pippi	Adult	Female
Paquita	Adult	Female
Carlotta	Adult	Female
Pepe	Adult	Male

Note. Subjects older than 8 years were classified as adults, and subjects between 5 and 8 years were considered subadults.

enclosures with outdoor and indoor areas. Capuchin monkeys were born in captivity, whereas spider monkeys were wild born but had extensive experience in the captive environment. Subjects were not deprived of food or water at any time. All subjects were accustomed to being in the testing room separated from group members (testing room size: 2 m × 2.3 m × 2.8 m for capuchin monkeys; an isosceles triangular base—3 m hypotenuse and 1.5 m height—with 3 m height for spider monkeys). All subjects had previously participated in experimental tasks, and they were always tested by the same familiar experimenter (the first author) during this study. However, none of the subjects had been previously tested on gaze-following tasks.

Materials

During the task, subjects were temporarily separated from their group members in the testing room. In some conditions, an opaque panel was placed outside the testing room, between the subject and the experimenter (see Figure 1). The panel (60 cm × 100 cm) was placed in one corner in such a position that the subject had to move a few steps toward that side of the testing room and move the head to follow the experimenter's gaze behind the barrier. Raisins or seeds were used to catch the subject's attention before starting a trial.

Procedure

Each subject was tested individually. In the few cases in which the subject was reluctant to be alone, another individual was present, and the trial was started only when there were no interactions between the two individuals. As in Braeuer et al. (2005),

the experimenter was outside the testing room in front of the subject. The experimenter was sitting and her eyes were about 100 cm from the ground and 60 cm from the mesh. Before the trial started, she gave one to three pieces of food (raisins or seeds) to the subject, one after the other. Then, she took another piece of food and held it in her fingers in full view of the subject half way between the subject's eyes and her eyes. The trial started when the subject was within the experimenter's reach (approximately 60 cm) looking at the piece of food. Consequently, subjects always looked in the experimenter's direction when she turned her head and gaze.

The study consisted of two experimental conditions and two control conditions, each composed of six trials. In the first experimental condition ("look-at-ceiling" condition), the trial started and the experimenter suddenly raised her head and looked for 10 s toward the upper and farthest corner of the testing room, at the subject's left side. After that, the experimenter gave the subject the food she had been holding in her hand during the trial, regardless of the subject's response. In the first control condition, the procedure was exactly the same as before, but instead of looking at the upper and farthest corner of the testing room, the experimenter looked for 10 s toward the subject and then gave the subject the food. To avoid intimidating the subject in this condition, the experimenter always avoided staring at the subject's eyes and instead looked at the subject's feet.

In the second experimental condition ("look-behind-the-barrier" condition), an opaque panel was standing vertically in front of the testing room, at one corner, close to the wall of the testing room and rotated around 45 degrees from the side of the testing room faced by the experimenter (see Figure 1). Although the subject did

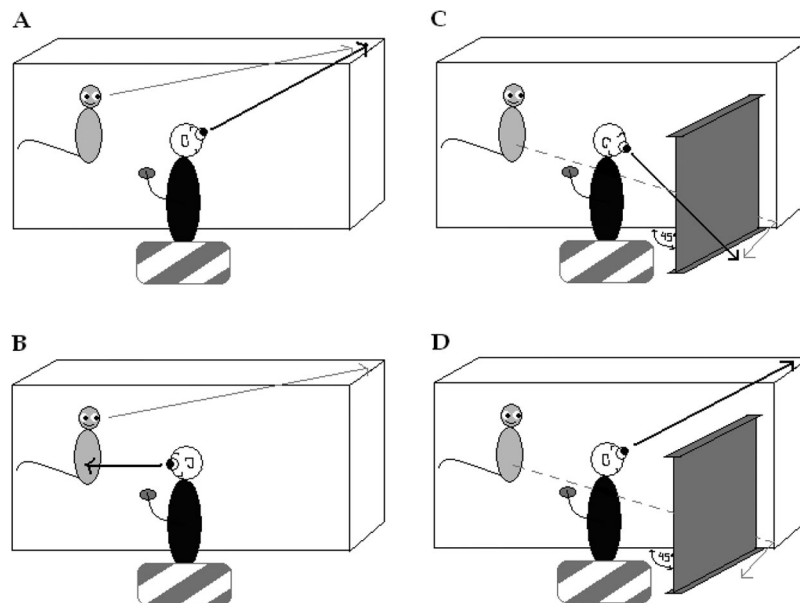


Figure 1. Diagram of the four different conditions: first experimental "look-at-ceiling" condition (A) and its correspondent control condition (B); second experimental "look-behind-the-barrier" condition (C) and its correspondent control condition (D). The black thick arrow indicates the direction of the experimenter's gaze during the trial; the gray thin continuous arrow indicates the direction of the subject's gaze that was subsequently scored; the gray thin dotted line indicates the movement that the subject must do before being able to look behind the barrier.

not have to move to any specific location to see whether the experimenter was looking behind the barrier, the position and the size of the panel allowed the subject to see *what* the experimenter was looking at only by moving into the right low corner of the testing room, bending its body and following the experimenter's gaze *behind* the barrier down to the floor. The procedure was as in the first experimental condition, but like in Braeuer et al. (2005), the experimenter looked for 60 s at a location on the ground behind the barrier. Moreover, the food was held visible on the side of the barrier opposite to that where the subject had to go to look behind the barrier, in a way comparable to that of the first experimental and control conditions, to prevent the subject only approaching the barrier and looking behind it to look at the food. The second control condition consisted of the experimenter suddenly looking at the upper and farthest corner of the testing room for 10 s (as in the first experimental "look-at-ceiling" condition), but in this second experimental condition, the opaque panel was present. The duration of this experimental condition (60 s) was longer than in the control condition (10 s) because the responses required had different duration. In the "look-behind-the-barrier" condition, subjects had to move to follow the experimenter's gaze and possibly search around the barrier, whereas in the "look-at-ceiling" condition, subjects could simply look at what the experimenter watched without moving. Consequently, the experimental conditions were not compared with each other, but each was compared with the corresponding control condition whose duration was matched.

Each subject participated in 24 trials (six trials per condition). On the first day, each subject participated in three trials of the "look-at-ceiling" condition, alternated with three trials for the correspondent control condition, with half of the subjects starting with the experimental and the other half with the control condition. On a following day, the same procedure was repeated. On a third day, subjects participated in three trials for the "look-behind-the-barrier" condition, alternated with three trials for the correspondent control condition, with half of the subjects starting with the experimental and the other half with the control condition. On a following day, the same procedure was repeated. We completed all "look-at-ceiling" trials prior to the administration of the "look-behind-the-barrier" trials because if no subjects performed the basic gaze-following response, it would have been pointless to test them in the "look-behind-the-barrier" condition.

Scoring and Data Analysis

All trials were videotaped and behaviors were scored from tapes. In all conditions, we scored simple looks and "looking back" behaviors and then calculated their mean frequencies. In the "look-at-ceiling" and its correspondent control condition, simple looks consisted of looking backward toward the upper and farthest corner of the testing room, where the experimenter was looking, whereas "looking back" behaviors consisted of looking toward the same corner, then at the experimenter, and then back at the same corner. In the "look-behind-the-barrier" and its correspondent control condition, simple looks consisted of looking at the location on the ground behind the barrier, where the experimenter was looking, from the location where it was possible to see what the experimenter was looking at; "looking back" behaviors consisted of looking behind the barrier, then at the experimenter, and then again back behind the barrier. In all conditions, "looking back"

behavior was scored only if the subject looked at the target location, at the experimenter, and back to the target location within a maximum of 5 s and without looking anywhere else in between. Because the experimental and control trials of the "look-behind-the-barrier" task differed in their duration, we calculated the behavioral rate (total frequency of behavior/total time) in each condition prior to comparing them.

A second observer, blind to the procedures and the goal of the study, coded 25% of all the trials to assess the interobserver reliability. Interobserver reliability was high (Cohen's $\kappa = 0.92$). Because the homogeneity of variance assumption was violated, we used nonparametric statistics to analyze effect of condition and time (Wilcoxon's test, with T standing for sum of ranks), as well as species (capuchin monkeys -n1- vs. spider monkeys -n2), age (subadults -n1- vs. adults -n2), and sex (males -n1- vs. females -n2; Mann-Whitney *U* test) on the subjects' performance. All tests were two-tailed and α level was set at .05.

Results

Spider monkeys looked up significantly more often in the "look-at-ceiling" condition than in the corresponding control condition ($n = 11$, $T = 66$, $p = .001$; see Figure 2). Neither sex nor age significantly affected the subjects' experimental frequency of simple looks (sex: $n_1 = 5$, $n_2 = 8$, $U = 18.5$, $p = .859$; age: $n_1 = 5$, $n_2 = 8$, $U = 14.5$, $p = .451$). The frequency of simple looks did not significantly vary between the first and the second sets of trials ($n = 9$, $T = 23$, $p = .992$). Similarly, capuchin monkeys looked up significantly more often in the "look-at-ceiling" condition than in the control condition ($n = 10$, $T = 55$, $p = .002$; see Figure 2). Neither sex nor age had any significant effect on the experimental frequency of simple looks (sex: $n_1 = 7$, $n_2 = 5$, $U = 10.0$, $p = .227$; age: $n_1 = 5$, $n_2 = 7$, $U = 15.0$, $p = .736$). The frequency of simple looks did not significantly vary between the first and second sets of trials ($n = 10$, $T = 29$, $p = .902$). When comparing spider monkeys' and capuchin monkeys' performance for the experimental condition "look-at-ceiling," no significant differences could be found for the frequency of simple looks ($n_1 = 12$, $n_2 = 13$, $U = 71.5$, $p = .739$). Finally, only one spider monkey performed "looking back" behaviors once (in the experimental condition).

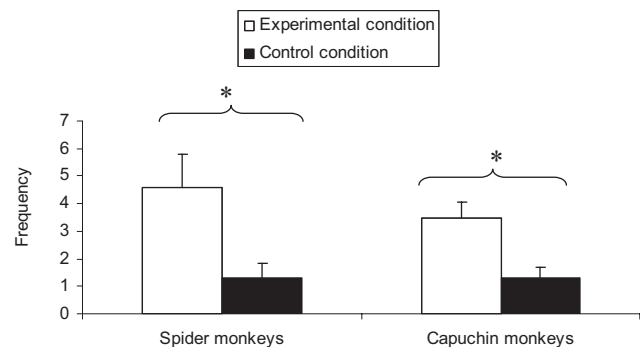


Figure 2. Frequency of simple looks at the ceiling in the experimental and control condition for spider monkeys and capuchin monkeys. Median and confidence intervals at 95% are shown. * Significant differences ($p < .050$) between conditions.

When the barrier was present, spider monkeys approached it and looked behind it only in the “look-behind-the-barrier” condition (see Figure 3). Consequently, they showed a tendency to look behind the barrier more in the experimental than in the control condition ($n = 5$, $T = 15$, $p = .063$). The frequency of simple looks in the experimental condition was not affected by either sex or age (sex: $n_1 = 5$, $n_2 = 8$, $U = 12.5$, $p = .293$; age: $n_1 = 5$, $n_2 = 8$, $U = 16.5$, $p = .608$). Moreover, the frequency of simple looks was not significantly different between the first and the second sets of trials ($n = 4$, $T = 7$, $p = .500$). In the “look-behind-the-barrier” condition, capuchin monkeys looked behind the barrier significantly more often than in the control condition ($n = 9$, $T = 45$, $p = .004$; see Figure 3). Neither sex nor age significantly affected the frequency of simple looks in the experimental condition (sex: $n_1 = 7$, $n_2 = 5$, $U = 16.5$, $p = .902$; age: $n_1 = 5$, $n_2 = 7$, $U = 11.5$, $p = .369$). The frequency of simple looks did not significantly vary between the first and the second sets of trials ($n = 7$, $T = 23$, $p = .188$). Spider monkeys and capuchin monkeys performed a comparable level of simple looks in the experimental condition “look-behind-the-barrier” ($n_1 = 12$, $n_2 = 13$, $U = 57.5$, $p = .251$). No “looking back” behavior was performed in either the experimental or control condition by either species.

Discussion

The present study investigated gaze-following behavior in two New World monkey species characterized by complex social systems. When presented with a human experimenter looking at a specific target location, both species looked at the same location significantly more often than when the experimenter was looking at the subject. In addition, capuchin monkeys followed the human’s gaze around barriers, and spider monkeys showed a tendency to do the same, but neither capuchin nor spider monkeys displayed any evidence of “looking back” behavior.

Our results on gaze following contradict those of a previous study in which capuchin monkeys failed to spontaneously follow the experimenter’s gaze (Itakura, 1996). Our positive results with both capuchin monkeys and spider monkeys support the idea that the ability to follow gaze is widely distributed among primates (Shepherd & Platt, 2008; Tomasello et al., 1998) and possibly among mammals (e.g., Kaminski et al., 2005; Miklosi et al., 1998) and birds (see Bugnyar et al., 2004). Even more important, both

species appeared to follow the experimenter’s gaze behind barriers. Capuchin monkeys moved and looked *behind* the barrier significantly more often when the experimenter was also looking behind the barrier than when the experimenter was looking at the ceiling. Spider monkeys’ frequency of looks behind the barrier did not reach significance, although five of 13 subjects repeatedly looked behind the barrier in the experimental condition, whereas no subject did it in the control condition. The capacity to follow conspecifics’ gaze behind barriers and past distractors might be advantageous by allowing individuals to better predict behavior and have more insight into complex social problems (Hare, Call, Agnetta, & Tomasello, 2000). Although basic gaze following is widespread among group-living primates (Shepherd & Platt, 2008; Tomasello et al., 1998), species living in complex social systems, such as spider monkeys and capuchin monkeys, might have faced evolutionary pressures to develop more complex forms of gaze following, consistent with a perspective-taking interpretation (Tomasello et al., 1999).

This high-level interpretation, however, needs to be tempered given that “looking back” behavior was absent in both species. The presence of “looking back” behavior in both great apes (Braeuer et al., 2005; Call et al., 1998) and long-tailed macaques (Goossens et al., 2008) might indeed reflect a consistent cognitive difference in gaze following between them and New World monkeys (including spider monkeys and capuchin monkeys). This interpretation seems to be supported by the results obtained by Hare, Addessi, Call, Tomasello, and Visalberghi (2003) on capuchin monkeys following a competitive paradigm. In that study, subordinate subjects adjusted their food retrieval strategies according to the dominant’s behavior, but in contrast to chimpanzees (Hare et al., 2000), they showed no evidence of perspective taking, retrieving food without taking into account what the dominant could or could not see (Hare et al., 2003). One possible explanation of our results might indeed be that New World monkeys do not engage in “looking back” behavior, perhaps indicating that they have no expectancies about the experimenter’s gaze (Butterworth & Cochran, 1980). However, it is also possible that a larger sample of individuals might reveal evidence of “looking back” behavior in spider monkeys and capuchin monkeys, as one spider monkey repeatedly engaged in “looking back” behavior in the experimental condition. If this were the case, a high-level interpretation of gaze following would seem more appropriate also for New World monkeys (Call et al., 1998). Indeed, studies following different procedures evidenced complex gaze-following skills also in New World monkeys, as recently shown in marmosets and tamarins (Burkart & Heschl, 2006; Neiwirth, Burman, Basile, & Lickteig, 2002; Santos & Hauser, 1999). Consequently, caution is needed when interpreting our results, and future studies should further investigate the possibility that “looking back” behavior and other behaviors indicative of high-level interpretation are present in both New and Old World monkeys.

From a theoretical point of view, the dichotomy between low-level and high-level interpretations of gaze following might be too simplistic (see Emery, 2000; Scerif et al., 2004). Subjects that solve multiple gaze-following tasks may do so by knowing what other individuals can or cannot see (so-called *Level 1 perspective taking*; Flavell, 1992) or by inferring how other individuals would see a particular display if they were located in a different location (so-called *Level 2 perspective taking*; Flavell, 1992). It is possible that New World monkeys have the skills to spontaneously follow

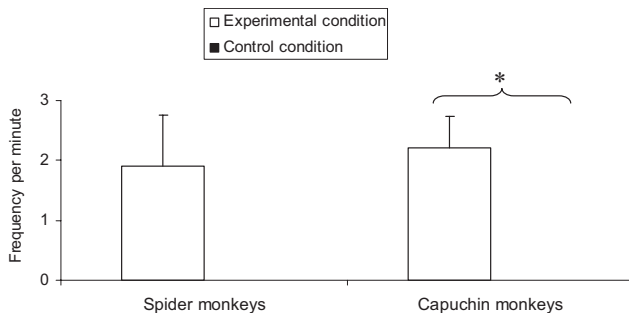


Figure 3. Frequency per minute of simple looks behind the barrier in the experimental and control condition for spider monkeys and capuchin monkeys. Median and confidence intervals at 95% are shown. * Significant differences ($p < .050$) between conditions.

the gaze of their conspecifics, even behind barriers, but they might lack Level 2 perspective taking. However, even the high-level interpretation applied to great apes falls short of certain forms of perspective taking and mentalizing based on attributing representational content to other individuals (see Call & Tomasello, 2005). Consequently, further studies should use other paradigms to further investigate the possibility of an intermediate level of gaze following in both capuchin monkeys and spider monkeys (see Anderson, Kuroshima, Hattori, & Fujita, 2005; Hare et al., 2003; Hattori, Kuroshima, & Fujita, 2007). Future experiments might also use conspecifics instead of humans as stimuli, although several studies have already failed to evidence major differences when using conspecifics or humans in gaze-following tasks (e.g., conspecifics: Emery et al., 1997; Tomasello et al., 1998; humans: Anderson & Mitchell, 1999; Braeuer et al., 2005).

Finally, sex had no effect on the subjects' performance in both experimental conditions. This confirms the results for the great apes (Braeuer et al., 2005), suggesting that gaze-following skills are advantageous for both sexes in a comparable way. In contrast to previous findings on the great apes (Braeuer et al., 2005), however, age had no effect on the subjects' performance in our study. However, a larger sample of subjects of various ages may reveal a developmental trend in spider monkeys' and capuchin monkeys' gaze-following behavior as reported in pigtail macaques (Ferrari et al., 2000).

To conclude, both spider monkeys and capuchin monkeys spontaneously followed a human experimenter's gaze and also reliably tracked her gaze behind opaque barriers. These results suggest that their gaze-following behavior cannot be explained only according to the low-level interpretation, and it possibly involves Level 1 perspective taking. Unlike the great apes, however, capuchin monkeys and spider monkeys might lack Level 2 perspective taking, as evidenced by the virtual absence of "looking back" behavior.

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