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Laurie R. Santos · Marc D. Hauser

How monkeys see the eyes: cotton-top tamarins' reaction to changes in visual attention and action

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Abstract Among social species, the capacity to detect where another individual is looking is adaptive because gaze direction often predicts what an individual is attending to, and thus what its future actions are likely to be. We used an expectancy violation procedure to determine whether cotton-top tamarins (*Saguinus oedipus oedipus*) use the direction of another individual's gaze to predict future actions. Subjects were familiarized with a sequence in which a human actor turned her attention toward one of two objects sitting on a table and then reached for that object. Following familiarization, subjects saw two test events. In one test event, the actor gazed at the new object and then reached for that object. From a human perspective, this event is considered consistent with the causal relationship between visual attention and subsequent action, that is, grabbing the object attended to. In the second test event, the actor gazed at the old object, but reached for the new object. This event is considered a violation of expectation. When the actor oriented with both her head-and-eyes, subjects looked significantly longer at the second test event in which the actor reached for the object to which she had not previously oriented. However, there was no difference in looking time between test events when the actor used only her eyes to orient. These findings suggest that tamarins are able to use some combination of head orientation and gaze direction, but not gaze direction alone, to predict the actions of a human agent.

Key words Gaze-following · Knowledge of agency · Action expectation · Cotton-top tamarin

Introduction

All animals, including humans, routinely encounter an assortment of moving objects in their natural environment. A small primate foraging in the canopy, for example, will encounter other conspecifics, branches blowing in the breeze, oncoming predators, and so on. Psychological objects represent an important subset of the moving objects encountered. Psychological objects are unique in that, unlike physical objects, they tend to move around on their own, and more importantly, have the capacity to act on other objects (Leslie 1994; Premack 1990; Premack and Premack 1997). The ability to identify psychological objects and predict their actions on other objects represents a highly adaptive capacity.

Do non-human animals make predictions about the actions of other psychological entities in their world? What cues do they use to predict the behavior of other individuals? One method used by our own species is to determine where another individual is looking. As adult humans, we understand that by focusing on where and what an individual is looking at, we are often able to infer what that individual is thinking, and thus, what that individual's future actions are likely to be (Baldwin 1991, 1995; Butterworth 1991; Tomasello 1995). As such, the direction of visual attention may function as an important predictor of an agent's future behavior, as well as his underlying intentions. The ability to use eye gaze to infer intentionality and belief is part and parcel of our capacity to attribute mental states to others (Baron-Cohen 1995 a, 1995 b).

In our own species, the ability to use eye gaze as a behavioral predictor emerges early in life. Baron-Cohen et al. (1993) found that by 3 years of age, children use the direction of gaze to predict both what an individual wants and where he is likely to act. This ability was examined in even younger infants by Ann Phillips and her colleagues, exploring whether 8- and 12-month-old infants recognize the importance of an intentional agent's visual attention using an expectancy violation paradigm (Spelke et al. 1995). The expectancy violation paradigm was developed

L. R. Santos (✉) · M. D. Hauser
Department of Psychology, Harvard University, 33 Kirkland St., Cambridge, MA 02138, USA
e-mail: lrsantos@wjh.harvard.edu,
Tel.: +1-617-4969331, Fax: +1-617-4963122

for use with preverbal human infants (Baillargeon 1994; Spelke 1994) and has been recently adapted for use with non-human primates (Hauser 1998; Hauser et al. 1996; Santos 1997; Uller 1997). The basic premise of the expectancy violation paradigm is similar to that of a magic trick (Spelke 1985; see Hauser and Carey 1998 for a more complete description). In this paradigm, subjects are shown an "unexpected" event which violates principles of the physical or psychological world. If subjects detect the violations, they are expected to look longer at the unexpected event than at a control event. As such, duration of looking can be used as a measure of knowledge (see Baillargeon 1994; Spelke 1994).

A. T. Phillips and her colleagues (Spelke et al. 1995) habituated infants to a scene with two toys sitting on a table in front of an actor whose gaze was fixed on one of the two objects. After staring for a few seconds, the actor then reached for this object. Following familiarization, the infants were presented with one of two test conditions. In one condition, considered "expected" from an adult perspective, the actor gazed at and then grabbed the new object. In the second, "unexpected" condition, the actor gazed at the original object, but then grabbed the new object. The expectation is generated on the basis of the observation that humans tend to act upon those objects previously attended to. Results demonstrated that 12-month-old infants, but not 8-month-olds, looked longer at the unexpected test event. A. T. Phillips and colleagues suggested that by 12 months of age, young infants are able to correctly predict an actor's future intentions based on the direction of gaze.

Although much is known about the developing child's capacity to use visual attention as a behavioral predictor, comparatively little is known about this capacity in other primate species (Cheney and Seyfarth 1990; Gomez 1991; Heyes 1998; Povinelli and Eddy 1996a, 1996b; Tomasello and Call 1997). There is evidence that, like human infants, several non-human primate species attend to the eyes when observing the behavior of other individuals. Adaptations for recognizing eye-like stimuli can be found throughout the animal kingdom and have clearly been demonstrated throughout the primate order (Baron-Cohen 1995b; Keating and Keating 1982; Kyes and Candland 1987; Redican 1975). Keating and Keating (1982), for example, illustrated that while viewing faces of conspecifics, humans, and other primates, rhesus monkeys (*Macaca mulatta*) selectively attend to the eyes over all other features of the face.

There is also evidence to suggest that some species of non-human primate attend to the direction of another individual's gaze (Call et al. 1998; Itakura 1996; McNelis and Boatright-Horowitz 1998; Mendelson et al. 1982). In most monkey species, staring directly into the eyes is recognized as threatening (see Redican 1975). Mendelson et al. (1982) demonstrated that by 3 weeks of age, infant rhesus macaques avert their eyes from a staring face, but maintain eye contact with faces looking away. In addition, neurophysiological research by Perrett et al. (1985, 1992) has demonstrated that areas of the macaque temporal cortex are dedicated to the detection of both head orientation and gaze direction. They have also demonstrated that stump-tail macaques (*Macaca arctoides*) are able to recognize when faces are looking at them using eye gaze direction independent of head orientation (Perrett and Mistlin 1990; Perrett et al. 1985; reviewed in Hauser 1996).

Another line of investigation indicates that at least some species of non-human primate are able to follow the direction of another individual's gaze and head orientation to an object in the environment. Itakura (1996) investigated the spontaneous gaze following behavior of 11 primate species – lemurs (*Lemur fulvus, L. macaco*), squirrel monkeys (*Saimiri sciureus*), capuchins (*Cebus capucinus, C. apella*), macaques (*Macaca mulatta, M. arctoides, M. nemestrina, M. tonkeana*), orangutans (*Pongo pygmaeus*), and chimpanzees (*Pan troglodytes*) – using a method somewhat similar to the one used by Butterworth and his colleagues to test human infants (Butterworth 1991, 1995). In this method, a human experimenter approaches a subject's cage and attempts to obtain eye contact. The experimenter then points with his hand and turns both his head and his eyes towards one side. Itakura (1996)found that while squirrel monkeys and lemurs showed a low percentage of head turning towards the side to which the experimenter was orienting (approximately 25%), all other species showed rather high percentages of gaze following (approximately 50% in macaques and capuchins, 70% in chimpanzees, and 100% in orangutans). These results suggest that several species are able to use a combination of pointing, head orientation, and eye gaze to determine where a person is attending. In addition, Tomasello et al. (1998) found that five primate species – chimpanzees, sooty mangabeys (*Cercocebus atys torquatus*), and rhesus, stumptail, and pigtail macaques (*M. mulatta, M. arctoides, M. nemestrina*) – are able follow the direction of a conspecifics gaze using a combination of head orientation and eye direction. Similarly, Emery et al. (1997) found that when they are viewing videotapes of conspecifics, rhesus macaques are able to use a combination of head orientation and gaze direction to orient their attention to a specific object or location. Lastly, Povinelli and Eddy (1996b) found that chimpanzees are able to use eye gaze alone to monitor where a human observer is looking. They found that in addition to following the gaze of a human actor to a desired location, chimpanzees are also able to use gaze information to track objects in areas outside their visual field, a more complex cognitive ability that only develops at 12 months of age in humans (Butterworth 1995).

In addition to evidence suggesting that several primate species can follow the direction of another individual's gaze, there is evidence that at least some species are able to use human gaze as a cue in an object-choice task. In a typical object-choice task, the location of a hidden food object is indicated by the orientational cues given by a human experimenter (e.g., pointing or gazing at the correct choice). Chimpanzees and at least one orangutan have been shown to use human gaze plus pointing and even gaze without head orientation to find hidden food rewards (Call et al. 1998; Itakura and Tanaka 1998). This capacity to use gaze alone as a cue, however, seems to be less prominent across the monkey species that have been investigated. J. R. Anderson and his colleagues (Anderson et al. 1995, 1996) found that although capuchins and rhesus macaques were able to use pointing to correctly identify the correct location, gaze and head orientation without pointing was not a sufficient cue. More recent evidence, however, suggests that at least one capuchin could eventually be trained to succeed in the task using all cues except gaze alone (Itakura and Anderson 1996).

Although some ape species have been shown to use the gaze of an experimenter as a cue in an object choice task, chimpanzees demonstrate striking failures to use visual attention in a slightly modifed task. Povinelli and Eddy (1996a) allowed chimpanzees to use a begging gesture to receive a food reward from a human researcher. They then set up experimental situations in which the subject was faced with a choice between two human observers from whom to beg. In most situations, the human observers differed in the way their eyes were oriented to the subject (e.g., facing or not facing subject, wearing a bucket over head, holding hands over eyes). Thus, the chimpanzees' task was to request food from the experimenter who was actually attending to them. The researchers found that chimpanzees were unable to perform this task. The subjects seemed to make no distinction between experimenters who were looking at them and experimenters who were not attending to them. These failures were interpreted to mean that the chimpanzees failed to understand that visual attention leads to knowledge.

At present, then, it appears that many non-human primate species are able to detect differences in the direction of gaze and some are even able to use visual attention as a cue during some object-choice tasks. It is not yet clear, however, whether such species are capable of using the direction of an individual's gaze to predict that individual's future actions. In this study, we investigated whether or not cotton-top tamarins (*Saguinus oedipus oedipus*) are able to use direction of gaze to predict a human agent's behavior using an expectancy violation paradigm similar to that used by A. T. Phillips and her colleagues (Spelke et al. 1995). Specifically, we asked whether tamarins make any predictions about people's future actions based on where they are looking. We reasoned that if tamarins are able to use gaze direction to predict which object an actor will act on, then, like 12-month-old infants, they should look longer at an action that is inconsistent with the direction of gaze, then an action that is consistent.

We were also interested in which features tamarins use to determine the direction of an individual's visual attention. In some of the studies cited above (Itakura 1996; Tomasello et al. 1998) head position and eye direction are perfectly correlated. Thus, when subjects respond appropriately to visual attention, it is difficult to tease apart the relative contribution of head position as opposed to gaze direction. For example, can tamarins judge where an individual is looking on the basis of eye direction alone or do they need a combination of head orientation and eye direction? To answer this, we tested tamarins in two different attention conditions: an "eyes-only" condition, in which the actor oriented towards the test object with only her eyes, and a "head-and-eyes" condition, in which the actor oriented towards the test object with both her head/body position and her eyes. We reasoned that if tamarins are able to use the eyes alone to determine the direction of visual attention, then they should look longer at the unexpected gaze-action test trial in both the head-and-eyes condition and the eyes-only condition. However, if tamarins require a combination of head orientation and gaze direction to determine where an individual is attending, then they should look longer at the unexpected-test trial in the head-and-eyes condition, but show no difference in looking time in the eyes-only condition.

Methods

Subjects

Subjects were 16 cotton-top tamarins (Table 1). Cotton-top tamarins are an arboreal New World monkey species native to the Colombian rainforests. Individual subjects were born at the New England Regional Primate Research Center and have been housed in a single homeroom at Harvard University for the past 5 years. Most subjects have previously been run in similar experiments (Hauser 1998; Hauser and Carey 1998; Santos 1997; Uller 1997). Each subject was tested in two sessions: a "head + eyes" (HE) session and an "eyes-only" (EO) session. Ten subjects received the HE session first while the remaining six subjects received the EO session first; the EO session for subject DD and the HE session for subject NC could not be used due to subject inattention and/or experimental error. The mean number of days between sessions was 10 (range 1–20 days). In both the HE and EO session, subjects received three familiarization trials and two test trials.

Table 1 Characteristics of individual subjects (*M* male, *F* female, *EO* eyes only, *HE* head + eyes)

Subject	Sex	Previous experience in other expectancy violation studies?	Order
AC	M	Yes	EO
DD	M	Yes	EO
DP	M	Yes	HE
EM	F	Yes	HE
ES	F	Yes	EO
ID	M	Yes	HE
JG	M	No	EO
JL	M	Yes	HE
MR	F	Yes	HE
NC	M	Yes	HE
RB	F	Yes	EO
RW	M	Yes	HE
SC	F	Yes	HE
SH	F	No	EO
SP	M	Yes	HE
UB	F	Yes	HE

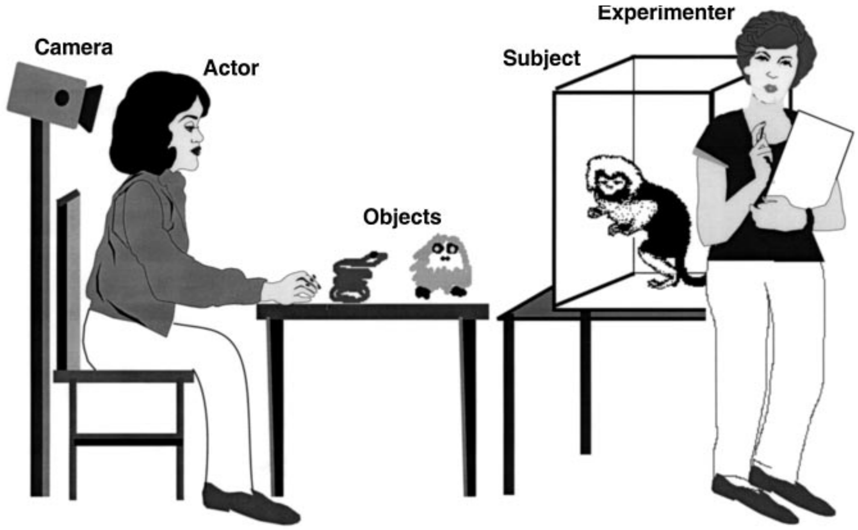


Fig. 1 Test apparatus and setup. *Subjects* sat inside the vortex *testing box* on a platform and could see out through the transparent Plexiglas front

Apparatus

During testing, subjects were placed in a transparent testing box (Fig. 1). The box was made entirely of Plexiglas and measured approximately 45 cm × 40 cm × 60 cm. Subjects sat inside the transparent triangular enclosure and were able to reach out through a small opening in the front wall. A foamcore occluder (60 cm × 60 cm) was placed at the front of the box and could be raised or lowered by the experimenter to prevent the subjects from seeing the experimental apparatus in between trials. Because of previous experimentation, subjects are familiar with the box and sit quietly and still inside the box for 30 min at a time.

A human experimenter dressed in a white lab coat (hereafter referred to as the "actor") sat on a chair placed approximately 1 m in front of the testing box. In front of the actor was a small table (approximately 0.75 m × 1.5 m). A videocamera was positioned behind the actor and was aimed at the subject's face to record looking time during the experiment.

Procedure

Head + eyes session

At the beginning of the HE session, subjects were taken from their homeroom and placed inside the testing box. Though they were allowed to see the actor sitting behind the table as they were placed into the testing box, subjects were unable to see the two stimuli (a plastic snake and a pink furry stuffed animal, both between 15–20 cm tall) when they first entered the testing room. After subjects were placed inside the box, the opaque foam core screen covering the testing box was raised to occlude the subject's view.

During the familiarization phase (Fig. 2a), each subject received three identical trials. Each trial began when the screen covering the subject's view was removed to reveal the actor seated in the chair and the two objects resting on the table on either side of the actor (e.g., pink animal to the actor's right, plastic snake to the actor's left). When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending to the display area, the actor abruptly turned head, body, and direction of gaze toward one of the two objects on the table (e.g., the snake). After 2 s of gazing, the actor reached with both hands and grabbed the object, holding it at eye level for 10 s. During this 10-s period, looking time was recorded. After 10 s, the screen was raised to occlude the subject's view. The object (pink animal or snake) oriented to and its location (left or right) were counterbalanced across subjects.

Following the familiarization phase, each subject received two different test trials: one "expected" and one "unexpected". The order of test trial types was counterbalanced across subjects. Both of these test trials ended with the actor reaching for the object opposite to the one grabbed during the familiarization trials. The expected-test trial (Fig. 2b) began when the screen was lowered to reveal the actor seated in the chair and the two objects resting on the table on either side of her. When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending, the actor abruptly turned head, body, and direction of gaze toward the object that *had not* been looked at during the familiarization (e.g., the pink animal). After 2 s of gazing, the actor reached with both hands and grabbed the *gazed-at object*, holding it at eye level for 10 s. During this 10-s period, looking at the display area was recorded. After 10 s, the screen was raised to occlude the subject's view.

The unexpected-test trial (Fig. 2c) began when the screen covering the subject's view was removed to reveal the actor seated in the chair and the two objects resting on the table on either side of her. When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending, the actor abruptly turned head, body, and direction of gaze toward the object that *had* been looked at during the familiarization trials (e.g., the snake). After 2 s of gazing, the actor reached with both hands and grabbed the *non-gazed-at* object (e.g., the pink animal), holding it at eye level for 10 s. During this 10-s period, looking at the display area was recorded. After 10 s, the screen was raised to occlude the subject's view.

Eyes-only session

The apparatus of the EO session was the same as in the HE session. The only difference was the use of two different stimuli: a gray furry stuffed bird and a plastic green alien toy (approximately 15–20 cm tall). As in the previous condition, these objects were chosen because they were novel, salient, and rather different in appearance from those used in the HE session. During the familiarization phase (Fig. 3a), each subject received three identical trials. Each trial began when the screen covering the subject's view was removed to reveal the actor seated in the chair and the two objects resting on the table on either side of the actor (e.g., bird to the actor's right, alien to the actor's left). When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending, the actor abruptly turned only *her eyes* toward one of the two objects on the table (e.g., bird). To make the change in gaze as salient as possible, the actor kept her eyes opened widely. After 2 s of gazing, the actor reached with both hands and grabbed the object, holding it at eye level for 10 s. During this 10-s period, looking at the display area was recorded. After 10 s, the screen was raised to occlude the

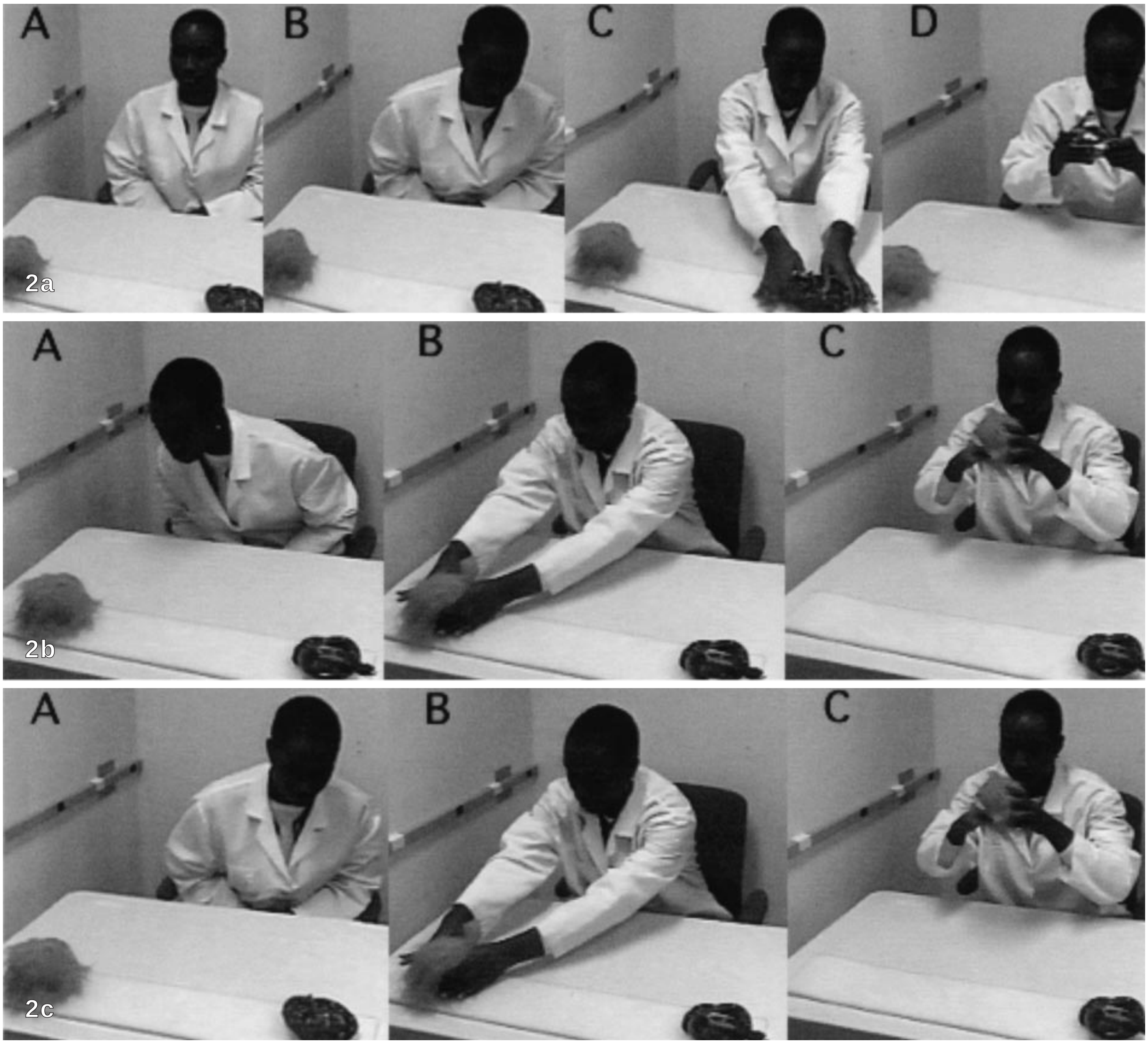


Fig. 2 **a** Familiarization phase. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns her head and gaze towards one object (*B*) and then reaches abruptly for that object (*C, D*). **b** Expected test event. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns her head and gaze towards the originally non-gazed at object (*B*) and then reaches abruptly for that object (*C*). **c** Unexpected test event. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns her head and gaze towards the object originally gazed at (*B*) and then reaches abruptly for the other object (*C*)

subject's view. The object (bird and alien) oriented to and its location (left or right) were counterbalanced across subjects.

As in the HE session, each subject received two different test trials during the EO session: the expected-test trial and the unexpected-test trial. The order of the test trial types was counterbalanced across subjects. Both of these test trials ended with the actor reaching to the object that she had not reached for in the familiarization trials. The expected-test trial (Fig. 3b) began when the screen covering the subject's view was lowered to reveal the actor seated in the chair and the two objects resting on the table on either side of her. When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending, the actor abruptly turned her eyes toward the object that *had not* been looked at during the familiarization phase (e.g., alien). After 2 s of staring, the actor reached with both hands and grabbed the *gazed-at object*, holding it at eye level for 10 s. During this 10-s period, looking at the display was recorded. After 10 s, the screen was raised to occlude the subject's view.

The unexpected-test trial (Fig. 3c) began when the screen covering the subject's view was removed to reveal the actor seated in the chair and the two objects resting on the table on either side of her. When the screen was lowered, the actor attempted to draw the subject's attention by staring at it and calling its name. Once the subject was attending, the actor abruptly turned her eyes toward the object that she had been looking at during the familiarization phase (e.g., bird). After 2 s of staring, the actor reached with both hands and grabbed the *non-gazed-at* object (e.g., alien), holding it at eye level for 10 s. During this 10-s period, looking at the display was recorded. After 10 s, the screen was then raised to occlude the subject's view.

Scoring looking time

The videocamera recording subjects' looking was set up so that the subject was in view of the videocamera whereas the experimental apparatus was out of sight. Videotapes could therefore be scored by coders blind to the experimental condition. Videotapes were recorded onto a Macintosh using a Radius Video Vision digitizing

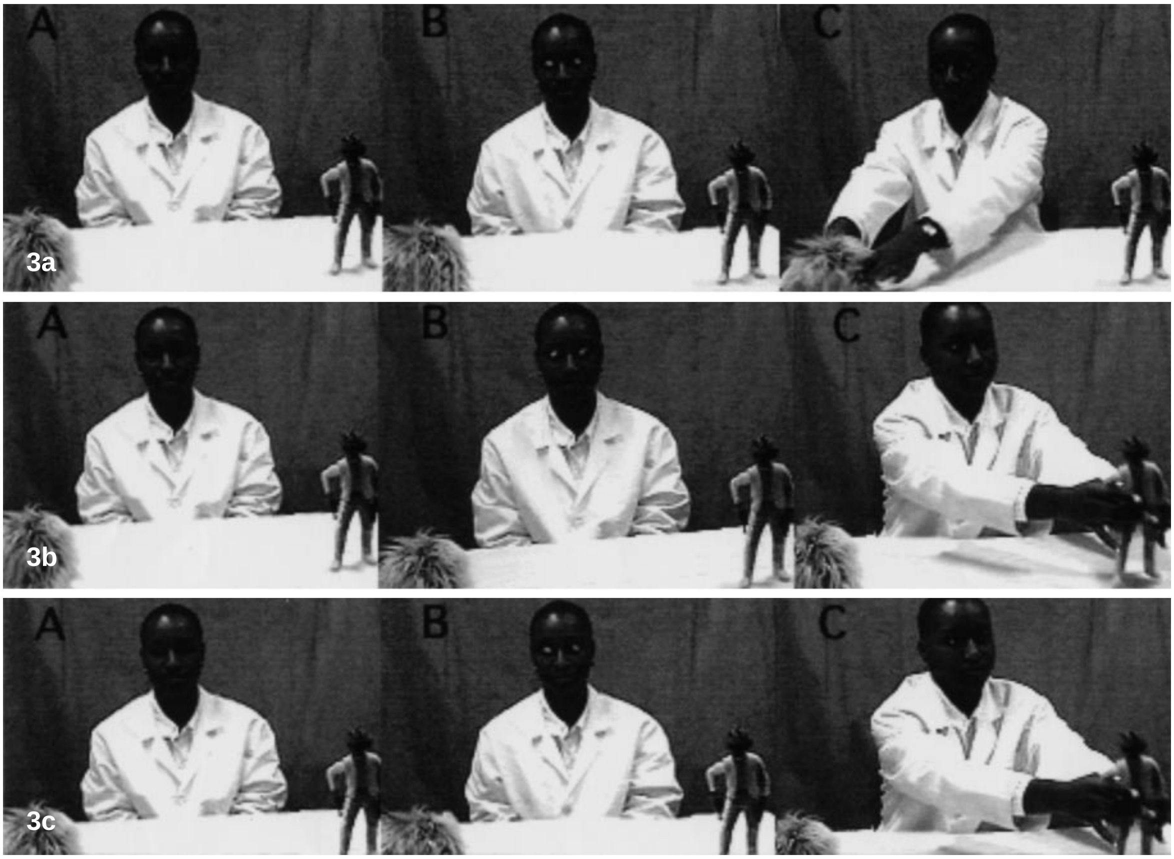


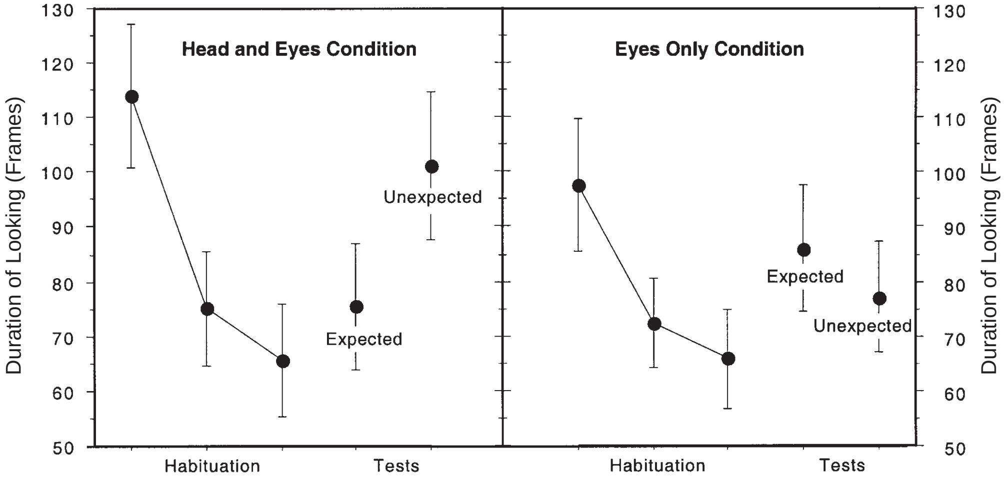
Fig. 3 **a** Familiarization phase. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns only her gaze towards one object (*B*) and then reaches abruptly for that (*C*). **b.** Expected test event. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns only her gaze towards the originally non-gazed at object (*B*) and then reaches abruptly for that object (*C*). **c** Unexpected test event. In *A*, the actor gains the attention of the subject by looking directly at him. She then turns only her gaze towards the originally gazed at object (*B*) and then reaches abruptly for the other object (*C*)

board, and were analyzed with Adobe Premiere 4.0 software. Two experimenters coded subject looking during each frame (30 frames = 1 s) of the 10-s looking period that followed each trial. The correlation between these two observers was $r = 0.98$ ($n = 10$ trials). "Looking" was operatively defined as a period of 5 frames or longer during which the subject's head was oriented towards the actor or the objects in the display.

Results

Figure 4 shows the mean amount of looking time across familiarization and test trials for each condition. A *t*-test between the first and last familiarization trial revealed that subjects habituated in the HE ($t_{(14)} = 5.55$, $P = 0.0001$) and EO conditions ($t_{(14)} = 2.28$, $P = 0.04$).

Fig. 4 Mean looking time across conditions for head + eyes (HE) session and eyes-only (EO) session in frames (*error bars* represent ± 1 SEM)



Looking-time scores for the test trials were entered into an ANOVA with condition (HE/EO) and test order (expected 1st/expected 2nd) as between session factors and test trial type (expected/unexpected) as a within session factor. There was no main effect of condition ($F_{(1,25)} = 0.03$, $P = 0.87$) or test order ($F_{(1,25)} = 0.46$, $P = 0.50$). There was, however, a main effect of test trial type. Subjects in both conditions tended to look longer at the unexpected-test trial (mean = 88 frames) than the expected-test trial (mean = 77 frames; $F_{(1,25)} = 4.16$, $P = 0.05$). In addition, there was an interaction between test order and test trial type ($F_{(1,25)} = 13.3$, $P = 0.001$). Subjects in both conditions looked significantly longer at the first test trial they saw.

Most importantly, there was an interaction of condition and test trial type ($F_{(1,25)} = 6.27$, $P = 0.02$). Although subjects in the HE condition looked longer at the Unexpected-test trial (98 frames) than the Expected test trial (70 frames), subjects in the EO condition showed no difference in looking across expected (84 frames) and unexpected-test trials (79 frames, see Fig. 4). This result was also demonstrated using non-parametric tests as well. During the HE condition, 10 out of 15 subjects looked longer at the unexpected-test trial (Wilcoxon sign rank test: $Z = 2.27$, $P = 0.02$). In contrast, during the EO condition, only 6 out of 15 subjects looked longer at the unexpected-test trial ($Z = 0.80$, $P = 0.43$).

Discussion

In both conditions, subjects demonstrated reliable habituation over the course of the first few familiarization trials. This suggests that subjects were familiar with the apparatus and set-up. In addition, in both conditions, subjects looked significantly longer at the first test outcome. This preference makes sense because the initial test trial is the first time that subjects see the actor grab the new object.

During the HE condition, subjects did in fact look longer at the unexpected-test trial than the expected-test trial, suggesting that witnessing the actor grab an object towards which she had not previously oriented was unexpected. This result raises two points. First, it suggests that during the HE condition, subjects are making a prediction about which object the actor will grab based on where she is orienting. Second, it suggests that this prediction can be made on the basis of head orientation and eye gaze alone. In other words, subjects are able to use a combination of head orientation and eye gaze to determine which object a human agent will grab.

In contrast to the HE condition, subjects in the EO condition showed no reliable difference in looking time for the expected and unexpected conditions. This result indicates that they find both EO test outcomes equally likely; when the actor grabs an object other than the one she looked at, it is apparently consistent with their expectations. One possible explanation for this finding is that for tamarins, eye gaze alone is not a sufficient cue for determining the direction of a human's attention. Because eye gaze alone is not sufficient, subjects in the EO condition fail to generate an appropriate prediction based on where the actor was looking, and fail to show a difference in looking time based on what the actor's next response might be.

Results suggest that tamarins are capable of using a combination of head orientation and eye gaze to predict the future actions of a human experimenter. This capacity stands in contrast to other species' apparent failures to use similar attentional cues in other paradigms (Povinelli and Eddy 1996 a; Anderson et al. 1995, 1996). There are two potential reasons for this difference. The first is that unlike previous experiments, our task did not require subjects to choose between two outcomes to obtain a food reward. Previous experiments with this tamarin population suggest that subjects appear to demonstrate knowledge in expectancy violation experiments that they fail to reveal when tested in a food choice paradigm (M. D. Hauser and T. Williams, unpublished work; Santos 1997). The other difference between our task and previous experiments is that our task required subjects to use visual attention to interpret behavior, not mental states. In this sense, our task differs from the experiments of Povinelli and Eddy (1996a) which do require subjects to infer mental states from the direction of an individual's attention.

Although tamarins are capable of using visual attention to predict a human actor's future behavior, eye gaze alone represents an insufficient cue for such predictions. Instead, it seems that the tamarins use information about head orientation and body posture to make these predictions. This interpretation makes some sense considering the differences in anatomy between humans and cotton-top tamarins. It is somewhat difficult (at least from the perspective of a human observer) to tell the direction of a tamarin's gaze solely from the direction of its eyes, since the tamarin sclera is not white, like a human's, but gray. It may therefore be hard for tamarins to detect the gaze direction of conspecifics and thus to use this cue to predict the future actions of other tamarins. If this is correct, it suggests that in tamarins there may have been no selective pressure on the ability to detect differences in the direction of visual attention using the eyes alone. Nonetheless, there may have been selective pressure on the capacity to use other more prominent features to detect the direction of conspecific visual attention (e.g., their large species-typical white tuft of hair). Consequently, if tamarins have evolved the capacity to use head orientation and body posture to predict the action of conspecifics, these are the same features that tamarins use when detecting the direction of a human's attention.

If our interpretation of the tamarins' behavior is correct, then several corollary predictions emerge. For example, species whose facial anatomy allows gaze to be an effective cue are more likely to use gaze alone as a feature for determining the direction of another individual's attention. Future work might profitably focus on the relationship between physiognomy, ecology, and social behavior.

A limitation of the present findings is that tamarins were required to discern the gaze and behavior of a human actor, rather than a conspecific. It may be that although tamarins are unable to discern the target of human gaze from the eyes alone, that such a capacity is fully functional when another tamarin's attention must be assessed on the basis of the eyes alone. As such, we are left with the possibility that tamarins will succeed in the eyes-alone condition of this experiment if tested with a conspecific actor. Nonetheless, these findings suggest that tamarins use a combination of head orientation and gaze direction to predict the future behavior of a human agent. This capacity parallels the achievements of 12-month-old human infants.

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