



## Articles

## Bonobos and chimpanzees infer the target of another's attention

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We examined the ability of bonobos, *Pan paniscus* ( $N = 39$ ), and chimpanzees, *Pan troglodytes* ( $N = 74$ ), to infer the target of an experimenter's visual attention in a series of three experiments. In each experiment subjects were first introduced to a novel object while an experimenter's (E1) visual access to this object was manipulated by (1) having E1 orient towards or away from the object, (2) positioning a visual occluder that did or did not block E1's view of the object, or (3) substituting a different experimenter for E1 during the introduction phase of the trial. After subjects were introduced to the objects in one of these ways, E1 vocalized excitedly while gazing ambiguously towards the previously introduced target object and a second location on the same visual plane. In each experiment we measured whether subjects looked at the object or the alternative target of the E1's gaze. We predicted that if subjects recognized when E1 was previously familiar with the object, they would search for an alternative target of his attention more frequently in these trials. In all three contexts, chimpanzees, and in one context, bonobos, behaved consistently with this prediction. These results are not easily explained by learning or behaviour-reading hypotheses because responses were never rewarded, few trials were conducted per subject, and the experimenter's behaviour was the same across experimental conditions at the moment subjects were required to respond. Therefore, similar to human infants, subjects most likely remembered what the experimenter had or had not seen in the past, allowing them to infer the target of his attention in the present.

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The social intelligence hypothesis predicts that social pressure to outcompete others for access to resources and mates has favoured individuals most skilled at predicting and manipulating the behaviour of others (Jolly 1966; Humphrey 1976; Krebs & Dawkins 1984; Byrne & Whiten 1988; Kummer et al. 1997; Dunbar 2003). One mechanism hypothesized to have evolved as a result of this pressure is an understanding of the psychological states of others. That is, an understanding of the underlying and unobservable psychological causes of behaviour. Such an understanding, even in rudimentary form, should afford considerable flexibility in predicting and interpreting others' behaviour (Krebs & Dawkins 1984; Byrne & Whiten 1988; Cheney & Seyfarth 1990; Kummer et al. 1997). Therefore, given the hypothesized role of social pressures on cognitive evolution in primates, experimentalists have tested whether primates, and in particular chimpanzees, are capable of modelling the psychological states of others (reviewed in: Povinelli & Preuss 1995; Heyes 1998; Maestriperi 2003; Tomasello et al. 2005; Call & Tomasello 2008; Hare 2011).

Most experimental work has examined whether primates have an understanding of others' visual perception (reviewed in: Call & Tomasello 2008; Hare 2011). This work has revealed that a variety of primate species can exploit a competitor's body or facial orientation when making foraging decisions (e.g. Flombaum & Santos 2005; Sandel et al. 2011), while many species are also capable of reliably co-orienting in response to a shift in another's gaze direction (reviewed in Rosati & Hare 2009). Experiments with great apes have ruled out low-level, reflexive explanations for these behaviours. Great apes follow others' gaze past distracting objects (Tomasello et al. 1999) and around visual occluders (Povinelli & Eddy 1996; Brauer et al. 2005; Okamoto-Barth et al. 2007). Moreover, experiments have demonstrated that chimpanzees are sensitive to what another individual can or cannot see in a variety of competitive situations (Hare et al. 2000, 2001; Brauer et al. 2007; Kaminski et al. 2008; Schmelz et al. 2011). Research outside the great apes has detected similar social cognitive abilities in a range of other species (Bugnyar & Heinrich 2005; Flombaum & Santos 2005; Hare & Tomasello 2005; Miklosi et al. 2007; Seed et al. 2009; Sandel et al. 2011).

Despite evidence that primates, and chimpanzees in particular, can assess what others can and cannot see, the ability to infer the target of another's attention may be a uniquely human trait

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(Tomasello & Haberl 2003; Moll et al. 2006; Moll & Meltzoff 2011). While current experimental data suggest that chimpanzees can establish when another individual can see them or other objects in the environment, there is no evidence that they understand that another individual can attend to different components of the visual environment. For example, a chimpanzee may know that a group-mate sees the same group of red colobus monkeys that he sees, but he may be unaware that while he is focusing on the number of vulnerable juveniles in the monkey troop, his groupmate is warily attending to the number of large males (and is not eager to join the hunt!). A variety of forms of coordinated social behaviour may be difficult without an understanding of another's visual attention. Consistent with this notion is the observation that as children develop an understanding of other's attention they also begin to engage in triadic interactions that provide the social context for language acquisition (Bruner & Watson 1983; Tomasello & Todd 1983; Akhtar et al. 1996; Tomasello 2003; Tomasello & Haberl 2003). However, the only experiment designed to test whether nonhumans understand the attentional focus of others found no evidence for these skills in a small sample of chimpanzees (Tomasello & Carpenter 2005). Therefore, it has been suggested that nonhumans, including the great apes, may not understand others' attention despite sensitivity to what others can and cannot see (Moll et al. 2006; Moll & Meltzoff 2011).

In the current experiments we address this hypothesis with a large sample of bonobos and chimpanzees. In three different contexts resembling human developmental paradigms (e.g. Tomasello & Haberl 2003; Moll et al. 2006), we measured whether bonobos and chimpanzees can use their knowledge of a human's previous experience when inferring what that human is emotively responding to in the present. Following the logic of developmental studies, we predicted that if apes could reason about the experimenter's attention, they would infer that his excited reaction referenced something novel in the environment (from the experimenter's perspective). That is, we predicted that subjects would identify the cause of the experimenter's reaction in light of his (and not the subject's) previous knowledge of the environment. Crucially, in each study the subjects could not respond differentially based on their own egocentric perspective since they had the same experience with the objects in all conditions. Moreover, few trials were administered per subject, and responses were never rewarded, minimizing the potential role of learning.

## EXPERIMENT 1

Experiment 1 tested whether chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, would be more likely to gaze past an object that a human experimenter gazed and emoted towards if (1) the experimenter had previously been oriented towards this object and been unresponsive to it, than if (2) the experimenter had been oriented away from the object. Excited emotional responses are typically about objects or events that are new to an individual, rather than objects or events that an individual is already familiar with (Akhtar et al. 1996; Tomasello & Haberl 2003). Thus, we predicted that if nonhuman apes are capable of inferring the target of another's attention, they should strategically search the environment for something that is new to the individual displaying an excited emotional reaction.

### Methods

#### Subjects

Thirty-six chimpanzees (22 male, 14 female, mean age = 12 years) and 21 bonobos (15 male, 6 female, mean age = 9 years) participated. Details regarding subjects' age, sex and participation are reported in the Supplementary Material (Table S1). All

chimpanzee subjects live and were tested at the Tchimpounga Sanctuary, Pointe Noire, Republic of Congo. Bonobo subjects live and were tested at Lola ya Bonobo, Kinshasa, Democratic Republic of Congo. For a more detailed description of these field sites see Wobber & Hare (2011). All subjects were familiar with humans through daily interactions including feeding and cleaning of the dormitories. The first experimenter (E1) was relatively unfamiliar to the subjects, and interacted with them primarily for the purposes of these experiments. This individual was equally familiar to the chimpanzee and bonobo subjects.

### Apparatus

Subjects were tested in a familiar dormitory room with metal grid walls. The experimenter sat at a stool (20 cm tall) behind a wooden table (46 × 40 × 80 cm, height, width, depth) with a sliding top. Objects used as stimuli included various colorful toys (Supplementary Material, Fig. S1) that were novel to all subjects at the time of testing. These objects were presented on two platforms (height = 107 cm) that were positioned 10 cm to the right and left sides of the table. All trials were recorded with a JVC Everio hard disk camcorder for subsequent coding.

### Procedure

The first experimenter (E1) sat across a table from the subject and delivered food pieces to keep the subject stationed for the first part of the trial. A second experimenter (E2) entered the room from the rear and placed a novel object on one of the two platforms positioned at the right and left sides of the table. E1's body was turned in profile to the table such that one of these platforms was in front of E1's body while the other was behind him. In one condition, E2 placed the object on the platform in E1's visual field (object familiar). In these cases E1 tracked the placement of the object visually (by orienting his head) so that it was clear that he had observed this event. However, E1 displayed no excitement or emotion at this time. In the other condition, E2 placed the object on the platform behind E1, and out of E1's view (object new). Thus, it appeared that E1 was unaware that E2 had entered the room and positioned this item behind him. Both events were equally visible to subjects. In all trials E1 then gazed in the direction of the object, mimicked surprise, vocalized emotively, and stared for 10 s (see Supplementary Material, Video S1). Therefore in the object new condition, E1 turned his upper body, oriented towards the object and vocalized, whereas in the object familiar condition, E1 adjusted his gaze (eyes and head) towards the object and vocalized.

### Design and coding

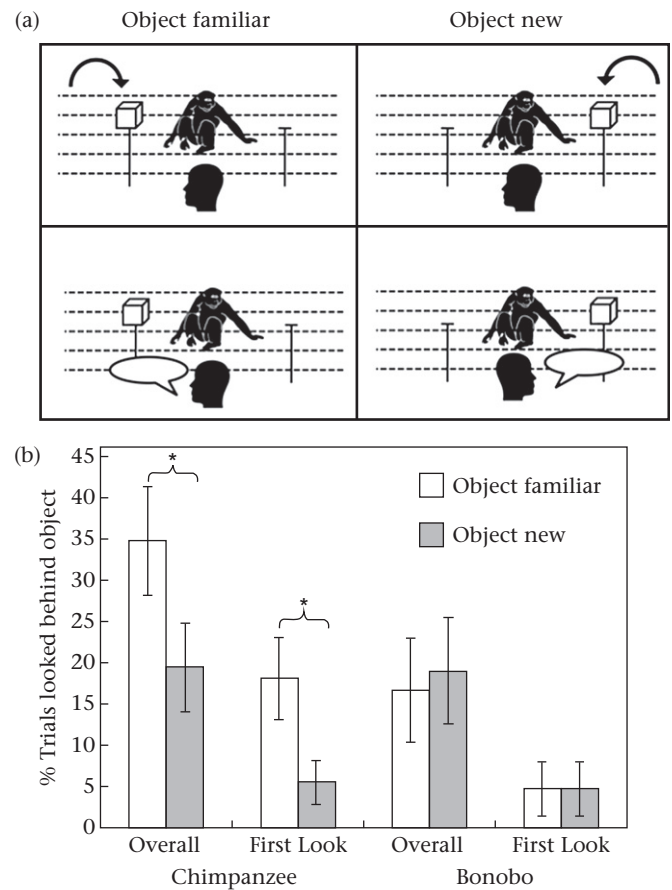
We conducted four trials with each subject. The location where the object was placed (in front of or behind E1) was counterbalanced within subjects and presented in an A-B-B-A order. The condition of the first trial and the direction that E1 was oriented throughout the session (left or right) was counterbalanced across subjects. A different object was used on each trial (Fig. S1), and the order that these objects were presented was the same for all subjects. E1 made two different vocalizations, a grunt-like ('uh') and an alarm-like call ('waa'), and each vocalization was paired with each experimental condition one time. We chose these vocalizations because they could be easily imitated by a human, loosely resemble emotive calls made by each species (van Hooff 1973; de Waal 1988; Bermejo & Omedes 1999) and both species demonstrated responsiveness to at least one of these cues beforehand in a related pretest (see experiment 3). As in previous studies using human vocalizations, the primary function of the vocalizations was to indicate excitement and to attract the subject's attention to E1, whose gaze could then be followed (e.g. Itakura et al. 1999).

Our dependent measures concerned whether subjects followed E1's gaze into space past the target object. Because the target object was positioned between E1 and the subject, but E1's line of sight continued into space past the subject, the subjects' body and/or head orientation could be categorized as either directed forward (into space where the object was positioned) or backward (into space behind the subject/object). Thus, if subjects rotated their body and/or head such that they were oriented into the space behind the object, we coded these events as backwards-directed looks. We analysed subjects looking behaviours using the following two measures: 'looked past object', which was scored as positive if subjects oriented backwards at any point during the 10 s period following E1's vocalization; 'first look', which was scored as positive if the subject's first head/body orientation following E1's vocalization was directed backwards. All trials were coded from video by a primary coder, and a subset of trials was coded by a reliability coder naïve to the hypothesis. Inter-rater reliability was calculated using Cohen's kappa (chimpanzees: first look:  $\kappa = 0.93$ ; looked past object:  $\kappa = 0.79$ ; bonobos: first look:  $\kappa = \text{NA}$  – 100% agreement; looked past object:  $\kappa = 0.80$ ). All statistical tests were one tailed to evaluate the directional hypothesis that subjects would look for an alternative target of E1's attention more frequently when E1 was familiar with the object, than when he was not.

### Results and Discussion

Analysis of both measures revealed that chimpanzees looked into space behind the object, along E1's line of sight, more frequently when E1 had previously seen the target object than when he had not (mean  $\pm$  SE percentage of trials, first orientation: object familiar:  $18 \pm 4.9\%$ ; object new:  $6 \pm 2.7\%$ ; Wilcoxon signed-ranks tests:  $Z = -2.18$ ,  $N = 36$ ,  $P = 0.01$ ; mean  $\pm$  SE percentage of whole trial: object familiar:  $35 \pm 6.6\%$ ; object new:  $19 \pm 5.4\%$ ; Wilcoxon signed-ranks tests:  $Z = -2.06$ ,  $N = 36$ ,  $P = 0.02$ ; Fig. 1). In contrast, bonobos followed E1's gaze past the object at equal rates between conditions (mean  $\pm$  SE percentage of trials, first orientation: object familiar:  $5 \pm 3.3\%$ , object new =  $5 \pm 3.3\%$ ; Wilcoxon signed-ranks tests:  $Z = 0.0$ ,  $N = 21$ ,  $P = 0.5$ ; mean  $\pm$  SE percentage of whole trial: object familiar:  $17 \pm 6.3\%$ ; object new:  $19 \pm 6.4\%$ ; Wilcoxon signed-ranks tests:  $Z = -1.23$ ,  $N = 21$ ,  $P = 0.89$ ; Fig. 1).

The results of this experiment suggest that chimpanzees may make inferences about the attention of others in ways similar to humans. When chimpanzee subjects saw an experimenter react in a surprised manner while looking in the direction of an object, they were more likely to search for something else that the experimenter was reacting to when this object was familiar (and uninteresting) to the experimenter than when the experimenter was seeing the object for the first time. To make this inference, subjects needed to track the experimenter's familiarity with the object (familiar or not) and use this information to infer the likely target of his gaze. Therefore, these results build on previous studies showing that chimpanzees ignore distracting objects when aligning their line of sight with another individual (Tomasello et al. 1999; Brauer et al. 2005) and know what others have and have not seen in the past (Hare et al. 2001; Kaminski et al. 2008). These results suggest that, in addition, chimpanzees may use this same type of information to make precise inferences about the target of another's attention. The negative results with the bonobos are subject to multiple interpretations. One possibility is that bonobos may not be able to assess the target of another individual's attention even though they readily follow the gaze of others (Brauer et al. 2005; Herrmann et al. 2010). However, negative results always warrant caution, and it is possible that bonobos may express similar skills to chimpanzees under different experimental conditions. Therefore, in experiment 2, we tested both species again in



**Figure 1.** (a) Apparatus and procedure used in experiment 1. One experimenter (E1) faced the subject in profile while another experimenter (E2) placed a familiar or new object in front of (left top panel) or behind (right top panel) E1's head. Later, E1 looked in the direction of the object and vocalized emotively (bottom panels). (b) Mean  $\pm$  SE percentage of trials in which the subject looked behind the object in experiment 1. \* $P < 0.05$ .

a new paradigm, based on a design in which bonobos have previously performed comparably to chimpanzees (Brauer et al. 2005).

### EXPERIMENT 2

Experiment 2 followed a similar design as experiment 1, but here we manipulated whether E1 was familiar with an object in his (and the subject's) line of sight by varying whether a curtain was positioned in front of or behind E1's head. This experiment was similar to experiment 1 in that it required subjects to reason about what the experimenter had and had not seen, but differed in the social information available for the subject to recall when inferring the experimenter's familiarity with the objects. Specifically, this experiment built on previous studies showing that great apes (including bonobos) understand the occluding properties of barriers on another individual's line of sight (Brauer et al. 2005; Okamoto-Barth et al. 2007).

#### Methods

##### Subjects

Thirty chimpanzees (12 male, 18 female, mean age = 9 years; Table S1) and 21 bonobos (14 male, 7 female, mean age = 10 years; Table S1) participated.

### Apparatus

An opaque barrier (180 × 180 cm) was positioned 90 cm away from and parallel to the front of the subject's enclosure. E1 sat behind a wooden table (46 × 40 × 80 cm, height, width, depth) approximately 80 cm away from the edge of the barrier facing the direction of two platforms (identical to experiment 1) that were placed 75 cm behind the barrier. The first of these platforms was positioned directly behind the edge of the barrier nearest to E1 such that subjects had a clear view of this platform when they were stationed at the table across from E1. The second platform was positioned 115 cm away from the first, such that subjects could not view this platform when they were stationed at the table unless the barrier was moved. Subjects could however move to another vantage point within the test room in order to view the second platform behind the barrier (Fig. 2). A JVC Everio hard disk camcorder was placed directly behind this platform so that subjects were visible on camera anytime that they moved into a position where they could view this platform. A curtain (180 × 90 cm) was positioned either in front of or behind E1, depending on the experimental condition. When this curtain was positioned in front of E1, it obstructed his (but not the subject's) view of the platforms,

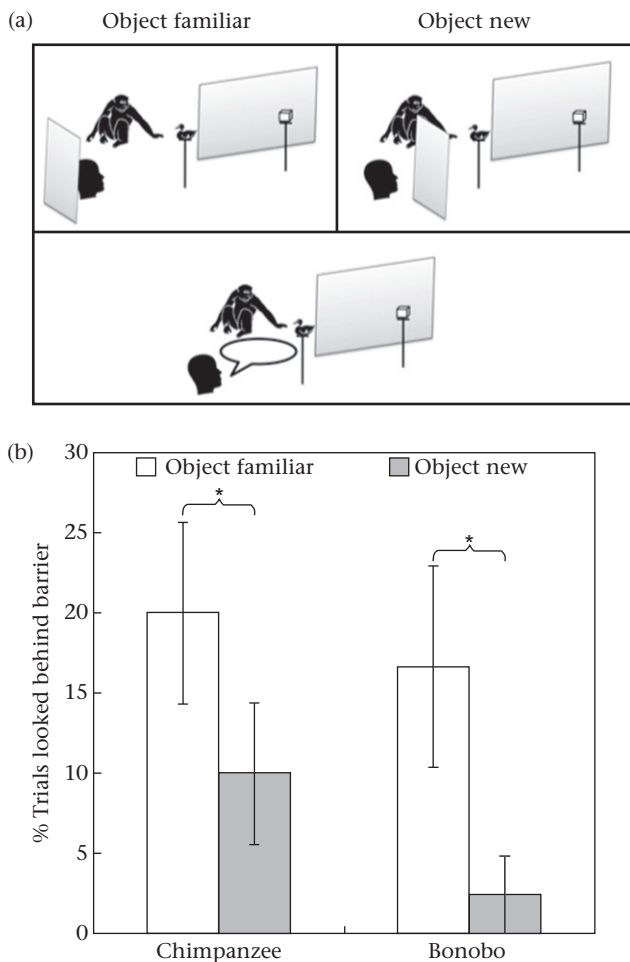
but it did not do so when placed behind him. Eight novel colorful toys were used as stimuli (Fig. S1).

### Procedure

E1 sat across from the subject, oriented to the table in profile and delivered food pieces to keep the subject stationed for the first part of the trial. E2 entered the room and placed novel objects on each of the two platforms positioned in front of E1, one behind the other, along the same visual plane from E1's perspective. The first object was visible to the subject from her position across from E1, but the second was hidden behind a barrier and only visible if subjects moved elsewhere in the room where they could peer around this barrier (Fig. 2, Video S2). However, when placing the second object, E2 briefly lifted the barrier allowing the subject to see that an additional object had been placed on the platform normally hidden behind the barrier. In the 'object new condition', E1 did not see either of the objects positioned because a curtain hanging in front of his face blocked his view. In the 'object familiar condition', E1 witnessed the objects being positioned because the curtain hung behind his head (so did not obstruct his view). Therefore, in the object familiar condition, E1 could see both objects (because they were positioned along the same plane from his perspective), but subjects could only see one object from their position across from E1 (the second object was occluded behind the barrier from the subject's perspective; Fig. 2). In all trials, E2 then removed the curtain next to E1. On trials when the curtain was positioned in front of E1, moving the curtain removed the visual barrier between E1 and the objects, allowing E1 to see the objects for the first time. On trials when the curtain was positioned behind E1, moving the curtain had no effect on E1's visual perspective. Once the curtain had been moved, E1 mimicked surprise and vocalized emotively while gazing towards the objects. Because both objects were located along the same visual plane relative to E1, subjects could not use E1's gaze orientation to infer which item E1 was looking at. Following the logic of experiment 1, we predicted that if subjects recognized when E1 was previously familiar with, and unresponsive to the objects, they would search for an alternative target of his attention more often in these cases than when E1 was encountering the objects for the first time at the moment of his surprised reaction.

### Design and coding

We conducted four trials with each subject. The location of the curtain (in front of or behind E1) was counterbalanced within subjects and presented in an A-B-B-A order. The condition of the first trial (curtain in front of or behind E1) was counterbalanced across subjects. Two different objects were used on each trial and the order and position of these items was the same for all subjects. E1 made the same two vocalizations as in experiment 1, and each vocalization occurred in each experimental condition once. The dependent measure was whether subjects moved to a location in the room that permitted them to view the object positioned behind the barrier. When subjects moved to an area of the room where they could see this object, they became visible to a video camera positioned behind the hidden object. Therefore, if a subject's face was visible from this camera angle during the trial, it was unambiguous that they searched for a new target of the experimenter's attention and they were coded as having moved to a location from which they could see the hidden object. All trials were coded from video by both a primary coder and a reliability coder naïve to the hypothesis (Cohen's kappa: chimpanzee:  $\kappa = 0.97$ , bonobo:  $\kappa = 0.82$ ). All statistical tests were one tailed to evaluate the directional hypothesis that subjects would look for an alternative target of E1's attention more often when he was familiar with the visible object than when he was not.



**Figure 2.** (a) Apparatus and procedure used in experiment 2. One experimenter (E1) faced the subject in profile while another experimenter (E2) placed objects on the platforms in front of E1. In the object familiar condition (left top panel), E1 saw E2 position the items because the curtain hung behind his head and did not obstruct his view. In the object new condition (right top panel), E1 did not see E2 position the objects because the curtain hung in front of his face and obstructed his view. Later, E2 removed the curtain and E1 looked in the direction of the object(s) and vocalized emotively. (b) Mean  $\pm$  SE percentage of trials in which the subject looked behind the barrier in experiment 2. \* $P < 0.05$ .

## Results and Discussion

Based on experiment 1, we predicted that subjects would search for an alternative target of E1's attention (out of sight behind the barrier) more often when E1 had previously seen the visible object than when he had not. That is, we predicted that subjects would search for something else that E1 might be reacting to more often when E1 had previously seen and been unresponsive to the visible object than when this object was new to him at the moment of his surprised reaction.

As predicted, both chimpanzees and bonobos searched behind the barrier blocking their view of E1's full line of sight more frequently when E1 had seen the initial object placement than when he had not (chimpanzees: mean  $\pm$  SE percentage of trials: object familiar:  $20 \pm 5.7\%$ ; object new:  $10 \pm 4.4\%$ ; Wilcoxon signed-ranks test:  $Z = -1.90$ ,  $N = 30$ ,  $P = 0.03$ ; bonobos: mean  $\pm$  SE percentage of trials: object familiar:  $17 \pm 6.3\%$ ; object new:  $2 \pm 2.4\%$ ;  $Z = -1.90$ ,  $N = 21$ ,  $P = 0.03$ ; Fig. 2).

In this experiment both chimpanzees and bonobos used information about what an experimenter had or had not seen to determine what the experimenter was attending to when gaze cues were not diagnostic. In contrast to experiment 1, both chimpanzees and bonobos behaved in a manner consistent with an understanding of others' attention. Both species were more likely to search behind a barrier occluding E1's full line of sight when E1 had previously seen (and been unresponsive to) the first object in his visual field than when E1 was seeing this object for the first time at the moment of his reaction. While the premise of experiments 1 and 2 was similar, these experiments utilized different dependent measures and required subjects to recall different information to infer E1's familiarity with the objects (e.g. body orientation versus the presence of a barrier blocking E1's view). Therefore, these results corroborate findings that great apes use multiple cues to infer what others can and cannot see and use this information flexibly when predicting or interpreting others' behaviour (Tomasello et al. 1999; Hare et al. 2000, 2001, 2006; Okamoto-Barth et al. 2007).

## EXPERIMENT 3

Experiment 3 was closely modelled after developmental studies of infants' understanding of others' attention in social contexts that have been linked to word learning. Tomasello & Haberl (2003) exposed 12- and 18-month-old children to two novel toys, which they played with in the company of two adults. One of these adults then left the room while the child played together with a third toy and the remaining adult. The absent adult then returned, looked in the direction of all three toys, which were aligned on a tray, expressed excitement and asked the child to give her the toy. In response to this request, infants selected the third toy, which was unfamiliar to the requester. Akhtar et al. (1996) used a similar procedure, but when requesting the toy, they did so by modelling a new word (e.g. 'Look, a modi!'). Following this game, children demonstrated knowledge that the new word referred to the toy that the requester had not seen before. Therefore, children kept track of which objects were familiar and new to an adult (even though all objects were familiar to the child), and they used this information to infer what the adult was attending to in an ambiguous situation. Thus, the combination of skills for reasoning about attention and skills for symbolic reference (word names) allowed the children to correctly infer the name of a novel object. In experiment 3 we tested whether nonhuman apes use information about identity (who has seen what) to infer what is new and familiar to different individuals in a manner similar to these studies of human children.

## Methods

### Subjects

Twenty chimpanzees and 11 bonobos participated in a pretest (see [Supplementary Material](#)). Twenty chimpanzees (12 males, 8 females, mean age = 7 years) and 18 bonobos (15 males, 3 females, mean age = 7 years) participated in the main test. Twelve of these chimpanzees and 10 of these bonobos had participated in the pretest. A second set of 20 chimpanzees (12 male, 8 female, mean age = 9 years) and 14 bonobos (7 male, 7 female, mean age = 10 - years) participated in a baseline condition, none of which had participated in the test condition.

### Apparatus

The apparatus for the pretest is described in the [Supplementary Material](#). We used the same objects from the pretest as test stimuli. Because all subjects had never physically manipulated any of these objects and only some had viewed them for a few seconds in the pretest through the top of a Plexiglas viewing panel, these objects were relatively unfamiliar to all subjects at the time of testing (approximately half of subjects had never seen these objects because they did not participate in the pretest). We used an opaque plastic bucket (diameter: 38 cm, height: 36 cm) with a  $50 \times 50$  cm cardboard lid to hide the objects during each trial. During the choice phase of each trial, we placed objects on a  $40 \times 15$  cm cardboard mat that allowed the subjects to manipulate the objects by touching the cardboard, while keeping the objects themselves out of reach.

### Procedure

In the pretest, subjects witnessed E1 look into two containers successively and respond to viewing the container's contents. At one of the containers, E1 vocalized either with a 'waa' or an 'uh' to indicate excitement (the 'waa' loosely mimicked an alarm bark while the 'uh' was loosely modelled after a grunt) while he showed no reaction to seeing the contents of the other container (see [Supplementary Material](#)). Subjects were then allowed to approach one of the containers to investigate its contents. The pretest served to verify that subjects preferred to view the contents of the container that elicited an excited reaction from E1. Chimpanzee subjects preferred to view the contents of the container that provoked E1's reaction for each of two vocal cues. Bonobos showed a similar preference but responded above chance to only one of the two vocalizations (the 'waa' call). For this reason, only one vocal cue was used with bonobos.

In two test conditions, E1 remained outside the room while E2 entered the room carrying the bucket (which contained a hidden toy) and a novel object, which was visible to the subject. E2 placed the bucket on the ground and positioned the object on the floor next to the bucket. In the 'object new condition', E1 remained outside the room while E2 knelt on the ground, visually inspected the object in front of the subject, and then left the room. In the 'object familiar condition', E2 left the room, E1 entered, knelt on the ground, visually inspected the object in front of the subject, and then left the room. Thus, in both cases the subject witnessed an individual inspect the object, but in one case this was E1, while in the other it was E2 (Video S3). In both conditions, E1 then entered, approached the bucket, peered inside and jumped as if startled while vocalizing excitedly. E1 quickly put the bucket down (lid intact) and moved to another area where he fed the subject. While the subject was distracted (the subject's back was turned while she received food from a window in the back of the room), E2 removed the visible object from the bucket and placed it at one side of the enclosure, then placed the bucket, lid intact, at the other side. Once these items were in position, E1 stopped feeding the subject, and

the subject was allowed to choose between inspecting the visible object (subjects could manipulate the object by moving the mat on which the object was positioned) or the bucket's contents (subjects could view the bucket's contents by displacing its lid). Once the subject had chosen, E2 allowed the subject to view or manipulate the object for about 5 s before she removed all stimuli from the enclosure. If a subject did not make a choice on two trials, the session was terminated and the partial data from the session were excluded from analyses (2 chimpanzees, 1 bonobo). These subjects were not retested in this experiment.

We conducted a baseline condition to measure apes' preferences for either viewing the hidden contents of a bucket, or inspecting a visible object (identical objects to the test) in the absence of any social cues from E1. Therefore, the baseline allowed us to assess whether subjects' choices in either condition of the test (object familiar, object new) deviated from apes' spontaneous preferences for investigating these objects. The procedure for the baseline condition was identical to the test with the exception that only E1 interacted with the objects and he never reacted emotively (with vocalizations or behaviours indicating surprise) while looking in the bucket. Thus, the object was temporarily displayed, placed in the bucket, and the subject was temporarily distracted while the object was taken out of the bucket and positioned identically to the test conditions. As in the test conditions, subjects were then allowed to choose between investigating the visible object and viewing the bucket's contents. As in the test condition, if a subject did not make a choice on two trials, the session was terminated, the partial data from this session were excluded from analyses (2 bonobos) and the subject was not retested in this experiment.

#### Design and coding

In the test and baseline conditions we conducted eight trials with each subject. In the test, the first four trials included two trials in which E1 was familiar with the visible object (object familiar) and two trials in which he was not (object new), and the condition for the first trial was counterbalanced across subjects. For chimpanzees, E1 made the same two vocalizations used in the pretest, and each cue was paired once with the object new and object familiar conditions in the first four trials for each subject. Because of species differences in the response to these vocal cues during the pretest, only the 'waa' call was used with bonobos (see [Supplementary Material](#)). The second four trials were identical to the first four trials except that the order of trial types differed. E1 recorded the subjects' choices online, and all trials were coded later by an individual naïve to the hypothesis. Inter-rater reliability was excellent (100% agreement for all measures in the test and baseline conditions). The two test conditions were compared with a one-tailed test to evaluate the directional hypothesis that subjects would search in the bucket more often when E1 was familiar with the visible object than when he was not. The test condition was compared to the baseline condition using a two-tailed test because we had no a priori prediction regarding differences between these conditions. Although here we describe this experiment last, both the pretest and test were completed 1 year before experiment 1 and 2.

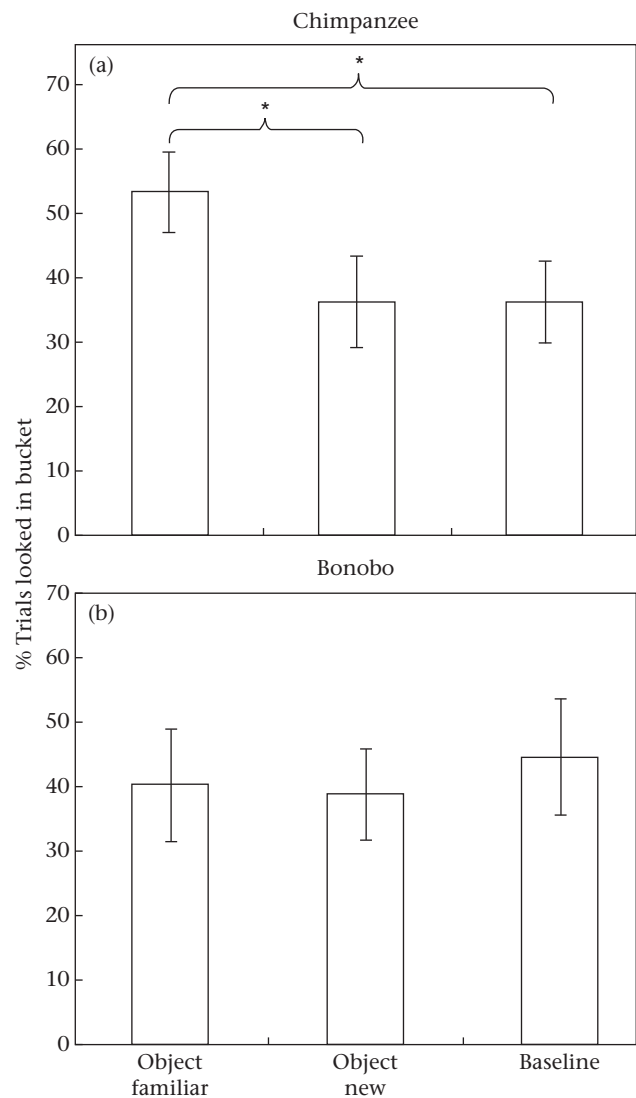
#### Results and Discussion

We predicted that subjects would search for something else inside the bucket that had elicited E1's reaction more frequently when E1 had previously seen (and not reacted to) the object that was placed inside the bucket than when this object was new to him (somebody else had inspected the object in view of the subject). Indeed, chimpanzees chose to view the contents of the bucket more frequently when E1 had previously viewed the visible object than

when he had not (mean  $\pm$  percentage of trials: object familiar:  $53 \pm 6.3\%$ ; object new:  $36 \pm 7.1\%$ ; Wilcoxon signed-ranks test:  $Z = -2.66$ ,  $N = 20$ ,  $P = 0.004$ ; Fig. 3). Chimpanzee subjects also searched in the bucket more often in the object familiar condition of the test than in the baseline condition (Mann–Whitney  $U$  test:  $Z = -2.05$ ,  $N_1 = N_2 = 20$ ,  $P = 0.04$ ). In addition, the chimpanzees searched in the bucket at similar rates between the object new condition of the test and the baseline condition (Mann–Whitney  $U$  test:  $Z = -0.07$ ,  $N_1 = N_2 = 20$ ,  $P = 0.95$ ).

In contrast, bonobos searched in the bucket at equal rates between test conditions (mean  $\pm$  percentage of trials: object familiar =  $40 \pm 8.8\%$ ; object new =  $39 \pm 7.1\%$ ; Wilcoxon signed-ranks test:  $Z = -0.40$ ,  $N = 18$ ,  $P = 0.34$ ). Comparison to the baseline condition revealed that neither test condition differed significantly from the baseline tendency to search in the bucket (Mann–Whitney  $U$  test: object familiar versus baseline:  $Z = -0.44$ ,  $N_1 = 18$ ,  $N_2 = 14$ ,  $P = 0.67$ ; object new versus baseline:  $Z = -0.44$ ,  $N_1 = 18$ ,  $N_2 = 14$ ,  $P = 0.67$ ).

In this experiment chimpanzees responded to E1's surprised reaction differently depending on whether E1 had previously seen



**Figure 3.** Mean  $\pm$  SE percentage of trials in which the subject looked in the bucket in experiment 3: (a) chimpanzees and (b) bonobos. \* $P < 0.05$  (comparisons with baseline were between subjects).

the object that was placed in the bucket or whether E1 was seeing this object for the first time at the moment he looked into the bucket. Specifically, chimpanzees were more likely to view the hidden contents of the bucket when E1 had previously seen (and been unresponsive to) to the visible object than when he had not. This suggests that the chimpanzees were searching for something else in the bucket that caused E1's reaction in these cases. These results parallel those from studies of 12- and 18-month-old children, who infer that such emotive responses are triggered by objects or events that are new, rather than familiar, to an experimenter. Importantly, human children use these skills in combination with skills for mapping symbols to objects in order to learn the names of novel objects. Our findings with chimpanzees suggest that some of these inferential processes were probably present in the last common ancestor of humans and the other great apes. Therefore, the human-unique process of language acquisition was probably scaffolded on sociocognitive skills already present in our lineage some 5–7 million years ago.

## GENERAL DISCUSSION

These results provide support for the hypothesis that our last common ancestor with chimpanzees and bonobos was able to assess the attentional states of others. In three contexts, chimpanzees, and in one context, bonobos inferred that an emotive response was elicited by something other than an object familiar to a human experimenter. These results are difficult to explain with low-level learning or online behaviour-reading hypotheses. First, each experiment manipulated the experimenter's experience with the objects in different ways (gaze direction, occluded visual access, or presence/absence). Second, few trials were conducted per subject and subjects' responses were never rewarded in any way. Third, at the moment the subjects had to infer the target of E1's gaze, there were no differences between the experimental and control conditions. Instead, subjects had to recall what the experimenter had seen in the past to interpret his current behaviour, yet they had no experimental training of any kind in this context (i.e. they did not know they 'needed' to remember what the experimenter had seen). Finally, subjects' responses were not egocentric since they were equally familiar with the objects between conditions. Therefore, similar to human infants, our subjects probably considered the experimenter's familiarity with different aspects of the environment to infer the target of his attention.

One implication of these findings is that while attentional perspective-taking was probably present in our last common ancestor with chimpanzees and bonobos, human brain development has evolved such that perspectival skills are expressed extremely early in ontogeny (Herrmann et al. 2007). This means these skills precede the initial and critical period of language acquisition in humans (Lenneberg 1967; Tomasello 2003). Humans begin following gaze within the first year of life (Scaife & Bruner 1975; Butterworth & Jarrett 1991; D'Entremont et al. 1997), while most chimpanzees do not spontaneously and reliably do so until 3–4 years (Tomasello et al. 2001; but see Okamoto et al. 2002, 2004; Tomonaga et al. 2004). This precludes the possibility of attentional perspective-taking in nonhuman apes in early infancy. Thus, by the age at which chimpanzees and bonobos begin to understand basic aspects of others' visual perspectives, human children already possess a sophisticated understanding of others' mental life. This ontogenetic difference between humans and other apes suggests that evolutionary developmental shifts (as opposed to the evolution of entirely novel traits) were responsible for the early emerging social skills of humans (Herrmann et al. 2007; Wobber et al. 2010).

Although both ape species expressed an understanding of others' attention, chimpanzees appear to have used these skills more flexibly than bonobos, modelling the experimenter's attentional perspective in all three paradigms. One intriguing possibility is that compared to chimpanzees, bonobos have less developed perspective-taking abilities because of an ontogenetic delay in their cognitive development. Indeed, compared to chimpanzees, bonobos show juvenilized patterns of growth (e.g. pedomorphic crania; Shea 1983; Lieberman et al. 2007) and social behaviour (Kuroda 1989; Wrangham & Pilbeam 2001). Moreover, recent studies suggest similar delays in cognitive tasks, with the effects of these delays persisting into adulthood (Wobber et al. 2010). Our results may be consistent with the pattern of delayed behaviour and psychological development previously observed in bonobos when compared to chimpanzees. However, the species difference we observed may also result from species differences in reactivity to human vocalizations. While we attempted to mimic vocalizations similar to those of both species (de Waal 1988; Bermejo & Omedes 1999), it is possible that bonobos found these human vocalizations less convincing than did chimpanzees. This possibility is supported by the results of the pretest in experiment 3, in which chimpanzees reacted to both vocalizations but bonobos only responded to one. However, the primary purpose of the vocalizations in these studies was to attract the subject's attention to the experimenter, whose gaze could then be followed. Across experiments, bonobos did respond to these vocalizations and behaved similarly to chimpanzees in experiment 2. In addition, bonobos have been shown to be more reactive to human gaze than are chimpanzees (Herrmann et al. 2010). Nevertheless, future studies will need to find ways to better control for these variables, perhaps through playbacks of conspecific vocalizations (Engh et al. 2006) or images (Hirata et al. 2010). Similarly, it is noteworthy that while we detected important differences between conditions in each experiment, subjects showed the predicted gaze-following response in a minority of trials in experiments 1 and 2 (~10–35% of trials). Therefore, the use of conspecific stimuli may also increase the overall response rate in these paradigms.

At present, the vast majority of studies documenting perspectival skills in animals have detected these abilities in contexts involving social competition for food (Hare et al. 2000, 2001, 2006; Flombaum & Santos 2005; Kaminski et al. 2008; Schmelz et al. 2011). Based on these results, some authors have argued that perspective-taking in nonhuman animals may be domain specific, and only deployed under competitive circumstances (Lyons & Santos 2006). However, our results support the prediction of Hare (2001) that competitive contexts are more likely, but not always necessary, to reveal social cognitive skills that can be applied flexibly across different social contexts. These findings also leave open the possibility that humans are unique in their tendency to share intentions cooperatively (Tomasello et al. 2005). Although our tasks were not competitive, they were also not particularly cooperative. Subjects in these studies probably used their perspectival skills in an exploitative manner. Therefore, while chimpanzees and bonobos may be capable of understanding others' attention, they may not use these skills to coordinate their attention with others, as is commonly observed in human infants. Lastly, while our experiments demonstrate that these species can infer where another individual is attending, it is unknown whether nonhuman apes make inferences about which aspects of the environment others are attending to (e.g. the size, shape, colour of a particular object).

Collectively, these data replicate and extend a growing body of research suggesting that the ability to represent others' psychological states is not unique to humans. Species of nonhuman apes, monkeys, lemurs, dogs and birds are all sensitive to social

information related to the perceptual states of others (Tomasello et al. 1998; Call et al. 2003; Flombaum & Santos 2005; Dally et al. 2006; Hare 2011; Sandel et al. 2011). Within the great apes, all species are sensitive to another's line of sight (Okamoto-Barth et al. 2007), and numerous studies indicate that chimpanzees (and now bonobos) recognize what others have seen in the past and exploit this information to their benefit (Hare et al. 2001; Kaminski et al. 2008; Schmelz et al. 2011). The current study adds to this knowledge by demonstrating that understanding others' attention is not unique to humans, does not depend on language, preceded language evolution and probably provided important cognitive scaffolding for language evolution in our species. Because our results implicate developmental differences in these skills between humans and other apes, we expect that comparative studies of cognitive development will be particularly important for identifying the basis of uniquely human social cognition (Hare 2011). Finally, because the methods developed here rely on spontaneous gaze-following measures, they may also be adapted easily for use with other species. These phylogenetic comparisons will be important for understanding the evolution of perspective-taking skills in animals (MacLean et al. 2011).

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### Supplementary Material

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