



## Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults



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Although previous studies have shown that many species follow gaze, few have directly compared closely related species, and thus its cross-species variation remains largely unclear. In this study, we compared three great ape species (bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, orang-utans, *Pongo abelii*) and humans (12-month-olds and adults) in their gaze-following responses to the videos of conspecific and allospecific models. In the video, the model turned his head repeatedly to one of two identical objects. We used a noninvasive eye-tracking technique to measure participants' eye movements, and used both conspecific and allospecific models as stimuli to examine their potential preference in following conspecific rather than allospecific gaze. Experiment 1 presented to great apes the videos of conspecific and human models. We found that all species followed the conspecific gaze. Chimpanzees did not follow the human gaze, whereas bonobos did. Bonobos reacted overall more sensitively than chimpanzees to both conspecific and human gaze. Experiment 2 presented to human infants and adults the videos of human, chimpanzee and orang-utan models. Both infants and adults followed the human gaze. Unlike adults, infants did not follow the ape gaze. Experiment 3 presented to great apes the videos of allospecific ape models. Consistent with experiment 1, chimpanzees did not follow the allospecific ape gaze, whereas bonobos and orang-utans did. Importantly, preferential following of conspecific gaze by chimpanzees (experiment 1) and human infants (experiment 2) was mainly explained by their prolonged viewing of the conspecific face and thus seems to reflect their motivation to attend selectively to the conspecific models. Taken together, we conclude that gaze following is modulated by both subject species and model species in great apes and humans, presumably a reflection of the subjects' intrinsic sensitivity to gaze and also their selective interest in particular models.

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Gaze following, defined as looking in the same direction as others after seeing their gaze direction, is one of the best studied social behaviours in comparative cognition. It functions in various ways depending on the species and context, from simply exploiting the same information that others have acquired to making inferences about others' intentions and knowledge (Hare, Call, & Tomasello, 2000). Gaze following has been documented in numerous species, including primates (great apes: Bräuer, Call, & Tomasello, 2005; Old World monkeys: Anderson & Mitchell, 1999; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Scerif, Gomez, & Byrne, 2004; New World monkeys: Amici, Aureli, Visalberghi, & Call, 2009; Burkart & Heschl, 2006; lemurs: Ruiz, Gómez, Roeder, & Byrne, 2009; Sandel, MacLean, & Hare, 2011; Shepherd & Platt,

2008), nonprimate mammals (dogs, *Canis familiaris*: Téglás, Gergely, Kupán, Miklósi, & Topál, 2012; goats, *Capra hircus*: Kaminski, Riedel, Call, & Tomasello, 2005), birds (ravens, *Corvus corax*: Bugnyar, Stöwe, & Heinrich, 2004; bald ibises, *Geronticus eremita*: Loretto, Schloegl, & Bugnyar, 2010) and reptiles (red-footed tortoise, *Geochelone carbonaria*: Wilkinson, Mandl, Bugnyar, & Huber, 2010). Although gaze following appears to be fairly widespread in phylogeny, studies have also documented its variation among closely related species. Thus, stump-tailed macaques, *Macaca arctoides*, follow gaze more frequently than other macaque species (Tomasello, Call, & Hare, 1998), bonobos, *Pan paniscus*, more than chimpanzees, *Pan troglodytes* (Herrmann, Hare, Call, & Tomasello, 2010) and human children more than great apes (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007), especially when only the model's eyes (not the head direction) serve as a gaze cue (Tomasello, Hare, Lehmann, & Call, 2007).

Moreover, rather than simply co-orienting with the model, in more complex settings in which individuals have to take into

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account the position and nature of visual barriers in relation to both the model and themselves, the distribution of gaze following among species appears more restricted. Thus, following gaze around barriers has been documented in apes, ravens, capuchin monkeys, *Cebus apella*, and spider monkeys, *Ateles geoffroyi*, but not in marmosets, *Callithrix jacchus*, and bald ibises (Amici et al., 2009; Bräuer et al., 2005; Bugnyar et al., 2004; Loretto et al., 2010; Tomasello, Hare, & Agnetta, 1999). Moreover, bonobos and chimpanzees, unlike orang-utans, *Pongo abelii*, take barrier opacity into consideration when following the gaze of others (Okamoto-Barth, Call, & Tomasello, 2007) and double-looks (i.e. looking back at the model's face after following her gaze and detecting nothing remarkable) have been observed in great apes and Old World monkeys but not in capuchin and spider monkeys (Amici et al., 2009; Bräuer et al., 2005; Scerif et al., 2004).

Taken together, these studies show that even though gaze following is displayed by numerous species, its expression in terms of strength and flexibility vary substantially among species. Data like these are crucial to be able to test evolutionary hypotheses linking gaze following with social and ecological factors that may contribute to explaining the differences between species, including the differences between human and nonhuman animals (Rosati & Hare, 2009). However, this sort of evolutionary analysis is currently hindered by two major difficulties. First, gaze following is modulated not only by the individuals' potential abilities but also by motivational or contextual factors. For example, in the previous studies with macaque species, the subjects preferentially followed the gaze of particular individuals depending on the social relationship with and emotional status of the model (Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008; Micheletta & Waller, 2012; Shepherd, Deane, & Platt, 2006; Teufel, Gutmann, Pirow, & Fischer, 2010). Most relevant for the species comparison is that many previous studies have used human models rather than conspecific models for pragmatic reasons, and thus it is possible that the species differ in the sensitivities to only human but not conspecific gaze. For example, Hattori, Kano, and Tomonaga (2010) found that chimpanzees followed the gaze of a conspecific but not of a human model when they were presented with the still pictures of those models (but see Itakura, Agnetta, Hare, & Tomasello, 1999), whereas human adults followed the gaze of both types of models. Ideally, when comparing two or more species, one should use a crossed design with two factors, subject species and model species, that is, presenting the models of both species to the subjects of both species.

Second, the dependent measure most often used in previous studies has been head-turning frequency owing to the difficulty in recording the eye movements directly. However, species may differ in their physical constraints to move their head, body and eyes. For example, orang-utans frequently move their eyes but not their heads to shift their gaze (i.e. sideways gaze; Kaplan & Rogers, 2002). Therefore, additional measurements based on eye direction alone may reveal gaze following that goes undetected when using more coarse measures based on head turning.

Developmental differences should also be taken into consideration when comparing species, especially species that may follow different developmental trajectories. Previous studies have shown that the sensitivity and flexibility of gaze following change with age in human and nonhuman primates. That is, human infants begin to follow the gaze of others from 3 to 6 months of age (D'Entremont, Hains, & Muir, 1997; Hood, Willen, & Driver, 1998) and establish a robust pattern from 1 year of age (Corkum & Moore, 1998; von Hofsten, Dahlstrom, & Fredriksson, 2005). Moreover, around 1 year of age human infants begin to follow gaze geometrically to regions beyond their immediate view (Moll & Tomasello, 2004). Similarly to nonhuman primates, human infants' gaze following is

modulated by motivational and contextual factors. For example, they preferentially follow the gaze of those who have looked towards interesting things versus nothing in the past (Chow, Poulin-Dubois, & Lewis, 2008), and take into account whether individuals have their eyes open or closed (Brooks & Meltzoff, 2002). In nonhuman primates, studies have shown that macaques and chimpanzees begin to follow gaze by around 1 and 3 years of age, respectively, and continue to increase the frequency of gaze following with age (Ferrari, Kohler, Fogassi, & Gallese, 2000; Tomasello, Hare, & Fogleman, 2001; but see Okamoto et al., 2002 for the earlier onset of gaze following in a chimpanzee). Moreover, macaques and chimpanzees display a relatively late onset for voluntary control of gaze following such as habituation to unreliable observers (Tomasello et al., 2001) and double-looks (Bräuer et al., 2005).

In this study we aimed to reveal the variation in gaze following among closely related species by addressing the above-mentioned issues. We used a crossed design with two factors, subject species and model species, and studied four hominid species, bonobos, chimpanzees, orang-utans and human infants (12-month-olds) and control adults (Fig. 1). We implemented a relatively simple setting to examine the basic performances of gaze following among species. That is, we measured the frequency of gaze following when each species was observing a human or conspecific model repeatedly turning his head to one of two identical objects. We adopted the eye-tracking method for two reasons: (1) to present controlled gaze cues of both conspecific and allospecific models on the computer monitor and (2) to rely on the eye movement measurement which is relatively independent of physical constraints. We examined whether species (1) showed any evidence of gaze following for each model species, (2) differentiated between conspecific and allospecific gaze, and (3) differed from one another in their overall gaze sensitivities (frequency and/or response time) when presented with either conspecifics or allospecifics. A previous study confirmed that the great apes did not differ from one another in their basic patterns of eye movement (Kano, Hirata, Call, & Tomonaga, 2011). However, the same study also confirmed that humans, especially infants (Hood & Atkinson, 1993), tend to shift their gaze less frequently (the fixations were 'stickier') than apes. Owing to this species difference and some procedural differences that existed for pragmatic reasons (e.g. the type of attracting stimuli), we did not compare great apes and humans in a single experiment. Experiment 1 presented to great apes videos of conspecific and human models. Experiment 2 presented to human infants and adults videos of human and allospecific ape models (chimpanzee and orang-utan). Experiment 3 returned to great apes and presented videos of allospecific ape models.

## EXPERIMENT 1

We examined the gaze-following responses in bonobos, chimpanzees and orang-utans when they were presented with a conspecific or a human model repeatedly turning his head to one of two identical objects. Based on previous studies using eye tracking (Hattori et al., 2010), we predicted that chimpanzees would preferentially follow the conspecific gaze rather than the human gaze. In addition, based on previous studies using a different behavioural paradigm (Bräuer et al., 2005; Herrmann et al., 2010), we predicted that bonobos would follow gaze, at least the human gaze, more frequently than chimpanzees. Finally, based on previous studies using behavioural paradigms (Bräuer et al., 2005; Okamoto-Barth et al., 2007), we predicted that orang-utans would follow the gaze of either conspecific or human models; however, it was unclear whether they would follow gaze differentially depending on the observed species.

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