



Responses of chimpanzees to cues of conspecific observation[☆]



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Recent evidence has shown that humans are remarkably sensitive to artificial cues of conspecific observation when making decisions with potential social consequences. Whether similar effects are found in other great apes has not yet been investigated. We carried out two experiments in which individual chimpanzees, *Pan troglodytes*, took items of food from an array in the presence of either an image of a large conspecific face or a scrambled control image. In experiment 1 we compared three versions of the face image varying in size and the amount of the face displayed. In experiment 2 we compared a fourth variant of the image with more prominent coloured eyes displayed closer to the focal chimpanzee. The chimpanzees did not look at the face images significantly more than at the control images in either experiment. Although there were trends for some individuals in each experiment to be slower to take high-value food items in the face conditions, these were not consistent or robust. We suggest that the extreme human sensitivity to cues of potential conspecific observation may not be shared with chimpanzees.

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A number of recent studies have shown that humans are remarkably sensitive to cues of conspecific observation when making decisions with potential social consequences. When images of 'watching eyes' are displayed, people are more reluctant to take an available resource for themselves (Burnham 2003; Haley & Fessler 2005; Burnham & Hare 2007; Rigdon et al. 2009; Oda et al. 2011; Nettle et al. 2012a; although see Fehr & Schneider 2010). They are also less likely to take from others (Baillon et al. 2013), and more likely to donate their own resources to a charitable cause, at least under some conditions (Ekström 2011; Powell et al. 2012). Moreover, they are less likely to litter, more likely to contribute to an honesty box, and more careful following recycling rules (Bateson et al. 2006; Ernest-Jones et al. 2011; Francey & Bergmüller 2012). The eye images used as cues of conspecific observation in these studies are very varied and often not at all realistic (see e.g. Burnham & Hare 2007; Rigdon et al. 2009; Powell et al. 2012). People do not report noticing the eyes or feeling less anonymous at the conscious level (see Oda et al. 2011; Francey &

Bergmüller 2012; Nettle et al. 2012a). This suggests that humans possess potent, automatic, easily evoked psychological mechanisms that modulate behaviour when conspecifics are watching. The functional significance of such mechanisms is presumably that conspecifics have the capacity to punish, or to use or spread negative reputational information, if they observe behaviours antithetical to their interests.

The phylogenetic origins of the mechanisms underlying the watching eyes effect have not yet been investigated, but they could be shared with other great ape species. Nonhuman primates show evidence of specialized psychological mechanisms for face processing that work in similar ways to those found in humans (Parr et al. 1998; Taubert & Parr 2012). Chimpanzees, *Pan troglodytes*, have a bias towards attending to faces more than other components in visual scenes, as humans do, although the bias is not as strong in chimpanzees (Kano & Tomonaga 2009), and the sequential fixations on the eye region of faces that are characteristic of humans are absent (Kano & Tomonaga 2010). Chimpanzees live in societies organized into dominance hierarchies that predict access to mates and food (Nishida 1979; Goodall 1986). The behaviour of chimpanzees indicates that they are acutely aware of their own position in the hierarchy (reviewed in de Waal 1986) as well as rank relations between others (Slocombe & Zuberbühler 2007). Subordinate chimpanzees are sensitive to whether a dominant can see a particular food item in their choice of whether to take it or not

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(Hare et al. 2000). This is due to the fact that dominants win out in scramble competition, and dominants may also punish subordinates for taking food items ahead of them (Jensen et al. 2007). Thus, there are reasons for expecting that there could be homologues of the watching eyes effect in chimpanzees.

Although the potential for third-party punishment may exist in some circumstances (e.g. von Rohr et al. 2012; but see Riedl et al. 2012; Engelmann et al. 2012), the data suggest that the predominant social risk for chimpanzees stems from direct second-party punishment rather than the broader suite of social and reputational consequences seen in humans. Thus, if there is a watching eyes effect in chimpanzees, it is most likely to be detectable in contexts in which the watching eyes represent cues that there might be a dominant individual nearby who is directly affected by the focal individual's actions, and who might administer second-party punishment.

Thus, to investigate a potential watching eyes effect, we devised a paradigm in which chimpanzees could take a food resource from the vicinity of either a larger-than-life stylized image of a chimpanzee face or an appropriate control image. We used stylized images rather than realistic ones to parallel the human experiments, in which highly stylized stimuli have been used. Our stimuli were black-and-white high-contrast renderings of a real photograph of a chimpanzee, similar to, although somewhat more detailed than, the Mooney faces used in human face perception research (Mooney 1957). Chimpanzees are known to recognize Mooney faces of chimpanzees as faces (Taubert & Parr 2012).

EXPERIMENT 1

We investigated the impact of displaying either a larger-than-life chimpanzee face or a matched control image on chimpanzees' latencies to take food items from an array containing items of both high value (peanuts) and lower value (peanut-sized pieces of carrot). Given that taking food in plain sight of a dominant individual can lead to punishment, we predicted that in the face conditions, individuals would be more hesitant to take the food items, as reflected in longer latencies. We also predicted the increase in latencies would be particularly marked for individuals who are subordinate within their social groups.

We additionally predicted that in the face conditions, chimpanzees might switch from starting with the normally preferred food item (peanuts) to the less valued option (carrots), on the basis that taking a high-valued item from in front of an unfamiliar conspecific is a riskier behaviour than taking a low-valued item. Again, we expected this to be particularly true of individuals of low rank. Our array was asymmetrical, with one end closer to the face or control image than the other. If our subjects interpreted the face image as a watching conspecific, we expected that they would prefer to take items from further away from the image in the face as compared to the control conditions. However, this might interact with dominance. Where dominant chimpanzees have access to two food items, one also accessible to a subordinate, and one only accessible to themselves, they tend to choose first the one accessible to both parties, so that they will end up with both items (Hare et al. 2000). Subordinates instead avoid the item also accessible to the dominant. Thus, here, we predicted that dominant individuals in the face condition might shift their preference towards starting with the items closest to the face image, so that they could secure these before moving to the proximal parts of the array. As a check for whether our face stimuli were noticed, we also recorded time spent looking towards the stimulus during each trial.

Methods

Subjects

Subjects were eight adult chimpanzees (four male, four female) from the same social group at Chimfunshi Wildlife Orphanage Trust, Zambia. These animals live in a large forested enclosure in a seminatural social group, but are habituated to humans, and are used to entering a building adjoining their enclosure for provisioning once a day. In the current experiment, individual chimpanzees voluntarily entered the building and remained inside for experimental sessions lasting up to 1 h before being released back into their enclosure. The dominance ranking of the eight individuals was assessed by K.A.C. on the basis of her longstanding experience working with these chimpanzees and independent interviews with the keepers who look after them. K.A.C. was blind to the results of the experiment when she provided her assessment. There was one pair of tied ranks. In this sample, all males outranked all females.

Both this experiment and experiment 2 were approved by Newcastle University Ethics Committee.

Experimental set-up

At the front of the experimental room was a concrete table 0.95 m high, half inside the room and half beyond a barred window onto a corridor whose gaps were sufficient for a chimpanzee to put a hand through. This allowed the subject to sit on the inner half of the table and reach through to take food items placed on the outer half by the experimenter (see Fig. 1). Experimental stimuli were displayed outside the experimental room on the wall facing the barred window at a distance of approximately 2 m and height of 1.75 m, offset to the right of the centre of the window from the chimpanzee's perspective. Trials were video recorded from a tripod-mounted camera at the same distance as the experimental stimuli but offset to the left.

Stimuli

To discourage habituation with repeated presentation, we created three different versions of a black-and-white cartoon-like chimpanzee face in Adobe Photoshop, using a stock photograph of a chimpanzee face as the starting point. One version, henceforth the small stimulus, featured just the upper face (eyes, nose and top of head) and measured 46 cm wide and 23 cm high, with an interpupillary distance (IPD) of 9 cm. The second version (large stimulus) was identical but measured 35 cm wide and 70 cm high (IPD = 14 cm). The third version (full stimulus) also included the muzzle and measured 43 cm wide and 35 cm high (IPD = 7.5 cm). The age and sex of the individual in the source image are not known. We sought to create apparent dominance by the image being slightly larger than life. For our full stimulus, implied bizygomatic breadth was 155 mm compared to actual male mean of 131.5 mm for chimpanzees from the Tai forest (Zihlman et al. 2008). For each stimulus, we created a control image by digitally cutting the image into 16 equal rectangles and inverting and shuffling these (see Fig. 1 for stimuli). Face and control stimuli were printed on durable fabric and attached to the wall using Velcro fastenings.

Experimental procedure

Prior to each trial, we laid out four shelled peanuts and four pieces of carrot of similar size to the peanuts, spaced 5 cm apart in an alternating line parallel to the barred window and 8 cm on the experimenters' side of it. The item closest to the experimental stimulus was always a peanut. Chimpanzees waited between trials in an antechamber from which the food items on the table were visible but, owing to the sightlines, the stimuli were not. At the beginning of the trial, the subject was admitted to the experimental

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