

# Visual co-orientation and expectations about attentional orientation in pileated gibbons (*Hylobates pileatus*)

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## Abstract

This study investigated attentional processes in a sample of captive gibbons. An initial aim of the research was to examine subjects' ability to co-orient with photographic images of both conspecific and human models. The gibbons' expectancies about the focus of another's attention was then also assessed, with an expectancy violation paradigm revealing subjects' sensitivity to an incompatibility between visual orientation and the position of a target object. The gibbons were exposed to two conditions; consistent sequences in which the stimulus individual directed attention towards a target object, and inconsistent sequences in which the model's attentional focus was incompatible with the location of this article. Analyses of the subjects' responses were made according to the direction of gazes and the time spent inspecting the depicted model in each of these conditions.

The results reveal a tendency for visual co-orientation with both conspecific and human models, suggesting that gibbons are competent in detecting the visual orientation of other species as well as their own. Furthermore, the subjects' tendency to look longer and check back to the depicted model in response to violations in the relationship between an agent and object (target appearing in an opposite direction to model's gaze), suggests that they possess some knowledge of how visual gaze direction relates to external stimuli.

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## 1. Introduction

Reports testifying to the gaze-following abilities of dogs (Hare and Tomasello, 1999), mountain goats (Kaminski et al., 2005) and birds (Ristau, 1991), have suggested the prevalence of this skill across the animal kingdom. However in spite of this, the identification of inter-species differences in this ability have yet to be satisfactorily clarified, with inconsistencies in the methodology employed and omissions in the species tested making it difficult to reach any definite conclusions (Povinelli, 1996; Heyes, 1998).

Extensive investigations of gaze-following in chimpanzees have provided a more comprehensive picture, and reveal that this species is relatively sophisticated in monitoring the attention of conspecifics and humans alike (Tomasello et al., 1998,

1999). Povinelli and Eddy (1996) provide evidence of chimpanzees following the visual gaze of a human experimenter to areas beyond their immediate visual field, an achievement which is not matched by human infants until around 18 months of age (Butterworth and Jarrett, 1991). Furthermore, it has been suggested that members of this species are capable of modifying their own body orientation when confronted with physical barriers which prevent them from pinpointing an experimenter's attentional focus (Tomasello et al., 1999).

Yet in spite of such robust testimony in the case of chimpanzees, there continues to be considerable ambiguity surrounding the abilities of other primate species. Studies involving haplorhines (sooty mangabey, Tomasello et al., 1998; macaques, Ferrari et al., 2000; diana monkeys, Scerif et al., 2004; capuchins, Itakura, 1996; squirrel monkeys, Itakura, 1996); strepsirhines (lemurs, Anderson and Mitchell, 1999) and great apes (orangutans, Itakura, 1996; Tomasello et al., 1998) reveal many inconsistencies. A number of studies report reliable gaze-following abilities amongst various species of monkey (Emery et al., 1997; Tomasello et al., 1998; Ferrari et al., 2000), and neurophysiological analysis of the temporal cortex suggests that these

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species possess neural mechanisms which could support such a behaviour (Perrett et al., 1985; Perrett and Emery, 1994). However in contrast to this, Itakura's (1996) comprehensive study of non-ape primates reported that failure to follow gaze was prevalent, and research has revealed that capuchin monkeys are often unresponsive to human eye gaze direction (Anderson et al., 1995; Itakura and Anderson, 1996).

Furthermore, there are some clear omissions in the types of species that have been tested, with the lesser ape species failing to be properly examined in studies of this nature. Myowa-Yamakoshi and Tomonaga (2001) provide a single report of a young gibbon's capability in detecting differences in visual direction, but no other studies exist regarding this ability. This may be considered particularly surprising given the phylogenetic similarity of these species to the much-studied great apes. The lesser apes are thought to have separated from the larger, great ape species only around 19–17 million years ago (Byrne, 1995), and thus insights into the behaviour of gibbons and siamang would seem to be important in pinpointing any divergence in the cognitive abilities of monkey and ape species. The brain physiology of the lesser ape species further suggests that they may bridge the gap between monkey and ape, with a pattern of convolutions in the cerebral cortex that is more complex than the former but less complex than the latter (Berkson, 1962).

Recent observations have begun to uncover the social existence of gibbons revealing that group interactions amongst conspecifics are much more common than traditional accounts have often portrayed (Bartlett, 2003). As arboreal primates, gibbons typically form monogamous pairs within small cliques of 2–7 animals (Burnie, 2001). As such they may be expected to closely monitor the behaviour of their social group. Yet the cognitive capabilities of these species remains open to question. Historically gibbon research has been limited, and our knowledge of this species continues to be restricted to a handful of reports: mirror self recognition behaviour (Ujhelyi et al., 2000; Hyatt, 1998), problem solving (Beck, 1967) and object manipulation (Cunningham et al., in press).

In the light of this, our first aim involved the use of newly established research techniques to determine whether a lesser ape species was capable of basic visual co-orientation behaviour. Recent developments in testing procedures have revealed the benefits of measuring primates' reactions to photographic material rather than live stimuli. The widespread use of this procedure has suggested that the presentation of static images can produce comparable reactions, whilst removing many of the problems associated with the use of unpredictable, live models in animal trials (Lorincz et al., 1999). Diana monkeys (*Cercopithecus diana diana*) and rhesus macaques (*Macaca mulatta*) are amongst the species shown capable of visual co-orientation in studies involving photo and film representation rather than real conspecifics (Scerif et al., 2004; Emery et al., 1997; Lorincz et al., 1999). In allowing greater control over the testing environment, such techniques also appear to overcome many of the methodological criticism traditionally directed at attention following studies.

Thus following similar methodology to that adopted by Lorincz et al. (1999) and Scerif et al. (2004) we presented sub-

jects with a static photograph of an individual whose body, head and eye orientation were directed towards a particular distal location. Subjects' responses to these stimuli were then analysed to determine whether they showed a tendency to track this depicted individual's attention towards this location in space. A positive result in this regard would indicate that the ability to track the attentional focus of others is a widely deployed response, and a tool utilised by the lesser ape species as well as their great ape relatives.

In a novel development of previous research, we also compared subjects' responses to conspecific and human models. Given current concerns regarding the use of human experimenters in visual co-orientation tests (Itakura et al., 1999; Povinelli, 1996), this comparison was designed to assess the subject's ability to interpret human eye gaze and to explore any differences in subjects' tendencies to co-orient with these two species.

In addition, in accordance with the work of Ferrari et al. (2000), we included a control condition to enable a comparison of subjects' responses to animate and inanimate objects. Discrepancies in the gibbons' responses to test and control conditions would suggest that co-orientation is not simply an instinctive reaction to the presence of a face-like stimulus.

In a second line of research, we utilised an expectancy violation paradigm, based on a design adopted by Scerif et al. (2004), to determine whether the gibbons were capable of a more sophisticated level of response. The basic premise of this design is that if an occurrence appears inconsistent with the subject's expectations then they will tend to exhibit checking behaviour and longer looking times. Santos and Hauser (1999) have shown that cotton-top tamarins spend longer inspecting an unanticipated sequence of events than an expected incident, whilst chimpanzees and diana monkeys have been found to exhibit re-inspection or checking responses when presented with an inconsistency in the position of an object and the gaze direction of an agent (Call et al., 1998; Scerif et al., 2004).

Thus in line with this work, we assessed subjects' abilities to detect an anomaly in the relationship between visual orientation and the location of a target by revealing an object in a position that was either consistent or inconsistent with the depicted individual's attentional focus. By monitoring responses in these two conditions we examined whether subjects were sensitive to incompatibilities, as would be evidenced by their exhibiting prolonged inspections and showing increased checking behaviour in this condition. In an extension of previous work in this area, we again investigated subjects' responses to both human and conspecific models.

## 2. Materials and methods

### 2.1. Subjects

The current study involved two adult pileated gibbons (*Hylobates pileatus*); Giava (a female aged 27) and Ipan (a male aged 30). The female gibbon is known to have been born in the wild, but has spent much of her existence in captivity. However the male is believed to have been captured very early in



Fig. 1. Examples of test stimuli (L-R): human, conspecific and inanimate conditions. Original test stimuli were full colour images.

infancy and hand-reared by humans (Paignton Zoo Environmental Park, personal communication). For the last two years the gibbons have been housed together at Paignton Zoo Environmental Park. The area they inhabit consists of an indoor enclosure (two equally proportioned, adjacent cages measuring 207 cm × 310 cm × 157 cm) and a large outdoor island which they are able to roam freely.

## 2.2. Stimulus materials

The stimuli were presented to the gibbons through the glass wall of their enclosure. Photographs were presented on a free-standing board (58 cm × 79 cm) directly outside the glassed area, with the height of the stimuli set at an appropriate eye-level for the subjects. The test photographs consisted of three conditions; conspecific (depicting a pileated gibbon also housed at the zoo, although not one of the subjects), human (depicting a human model), and control (depicting an inanimate object, a white box with two adjacent black spots). See Fig. 1 for examples. There were five different models used in total; a woman and a man, a male and a female conspecific, and one example of an inanimate model. All of these models were unfamiliar to the subjects.

Each of the animate individuals was photographed whilst looking intently towards a distal location either to the right or to the left of them. Since research highlights the significance of body, head and eye cues in the detection of gaze direction (Perrett et al., 1992; Lorincz et al., 1999), it was important that each of these elements provided a consistent indication of visual orientation. In order to ensure that the direction of attention of the stimulus individuals was extremely clear a large number of images were taken with the most appropriate example of each model chosen for use in the study. The positioning of the control stimulus in the photograph was aligned so that it was clearly oriented to the left or the right, in a way analogous to the animate conditions. Selected pictures were cropped so that they

depicted only the upper torso and head region of the stimulus individuals and were also enlarged to A3 size (42 cm × 30 cm) so that they were approximately equivalent to the real life size of the individuals. In order to control for directional effects the photographic negative of each of the models was reversed. This produced a second set of stimuli which were exact duplicates of the originals except that the individuals' attention was oriented to the laterally opposite location.

The test material was then modified further, with two identical cardboard strips added to the left and right side of the stimulus individuals. A photograph of a target object was mounted on one of these extensions. In replication of the work of Scerif et al. (2004) together with the studies of Emery et al. (1997) and Santos and Hauser (1999), the target object chosen was a novel toy. In the consistent trials this object was positioned approximately 1 m from the model and in a location which was in line with this individual's gaze. However in the inconsistent trials the location of the toy was reversed so that it occupied a corresponding position on the opposite, unattended strip. During the first phase of the trials this target object was concealed, with two identical white sheets covering the extended strips so that only the stimulus model could be seen. These occluders were subsequently removed during the course of testing.

In order to minimise any habituation effects arising from repetitive exposure to the same stimuli the subjects were also presented with various non-test stimuli depicting birds, flowers and other common zoo scenes. Subjects' responses were captured on a video camera (Panasonic NV-GS70B) which was mounted on a tripod and positioned immediately above the experimental stimuli. A stopwatch was also utilised in the study in order to provide an exact timing of the sequence of events.

## 2.3. Procedure

Trials were conducted over a period of 2 months during July and August 2004. Subjects were tested within their enclosure and

given access to both the indoor and the outdoor area throughout the study. The subjects' enclosure was located in a restricted access area, which was inadmissible to the visiting public. Thus, it provided an ideal arena for testing, with relative freedom from the distraction of zoo visitors.

It has been suggested that gibbons exhibit a shyness and lack of motivation, which makes them less than ideal as experimental subjects. Berkson (1962) provides evidence that such obstacles to testing can be offset by providing a familiar, external testing environment and by ensuring that the subjects are not performing in isolation from their peers. Such considerations helped inform the testing environment for the current study.

The experiment did not cause any disruptions to the subjects' normal feedings regimes and the zoo staff continued to provide the subjects with their standard diet twice daily. Subjects were also able to join and cease participation in the study at will and no food reinforcements were offered as inducement for testing. As a result of these circumstances, there was considerable variability in the number of trials per session, with totals ranging from one to five per day. Consecutive trials were separated by variable time delays according to the subjects' attentiveness towards the test stimuli.

The photographic stimuli were prepared prior to testing, with test images arranged face down in separate stacks according to the visual orientation and the model each depicted. The experimenter was unaware of which stimuli conditions were contained in each stack. The division of the stimuli into groups ensured that whilst remaining unaware of the presentational order of conditions, the experimenter could avoid selecting the same stimulus individual in more than two consecutive trials, or a sequence of three or more conditions in which the model's gaze direction was the same. Test images could also be interspersed with non-test stimuli. Each photograph was separated by a white coversheet concealing the image until the commencement of a trial. The operation of removing the coversheet was performed from a position behind the free-standing board, where the test image could not be seen. In this way, the experimenter remained blind to the condition presented in each trial. A record of the presentational order of trial conditions was made subsequent to testing, in preparation for the later analysis.

Initial observations of the subjects' positioning relative to the equipment were made in order to determine when they were in an appropriate position for testing. Trials did not commence until subjects had good visual access of the testing materials and occupied a site which allowed them to be captured on the video camera. In addition, it was necessary that the subjects were attentive to the test materials and were at a sufficient distance away from their mate to ensure minimal distractions. When these criteria were met, the stopwatch was set, signalling the beginning of the trial.

The typical trial lasted for 10 s. Test trials commenced with the removal of the central white coversheet to reveal a test image of a stimulus individual gazing towards a distal location. After 3 s, the covers concealing the white strips were simultaneously removed revealing an object in a position that was either consistent or inconsistent with the depicted individual's line of gaze. Trials were timed by a stopwatch providing an audible tone to

guide the experimenter as to the exact interval at which the object should be uncovered. The experimenter occupied a discrete position behind the board and its support and attempted to remain out of the gibbons' visibility throughout testing. Attempts were also made to minimise any noise distractions during the procedure.

#### 2.4. Coding

An experimenter, who was blind to the presentational order of treatment conditions, made initial assessments of the subjects' behaviour during testing. Following methodology developed by Lorincz et al. (1999) and Scerif et al. (2004), the coder was provided with footage of the subjects' responses as recorded during test trials. This film included an audio commentary detailing the trial number and the precise timing of each stage of the procedure. In this initial phase of coding the experimenter was not informed of the condition-type presented in each trial, and this could not be gleaned from the video footage in which only the subjects themselves were captured.

The video screen was divided into four separate sections, the quadrants relating to the lower left and lower right regions of the screen (target and anti-target areas), a central section (reflecting eye gazes directed at the stimulus model), and an "elsewhere" category (including the lower middle and upper regions). For the first stage of the trial, comprising the first three seconds, the scorer coded subjects' initial inspections on presentation of the model and the duration of all inspections made during this period according to whether they were directed towards each of these four locations. Since adjustments to head orientation were necessary in order to co-orient with the depicted individual's gaze, attributions were based on both head and eye cues being clearly directed to a particular zone. A single inspection was defined as a fixation in which the subject's head orientation and eye gaze were static for a period exceeding 80 ms (or two frames). Thus visual scans were not included in the analysis. The number of consecutive video frames in which the subject's head and eyes pointed towards a particular region was assessed to determine the duration of each inspection. This process was repeated for the second stage of the trials with the scorer coding the subjects' first glance on exposure to the target object and all subsequent inspections until the end of the 10-s trial. The definition of a single inspection and the calculation of the duration of a glance followed exactly the same principles as that outlined for the first stage of the trials.

On completion of this process of blind coding the directions of inspections were re-classified taking into consideration the particular condition presented in each trial, as recorded in test documentation. Thus inspections were re-coded according to whether they were directed towards the 'target' location (the direction in which the stimulus individual was gazing), the 'anti-target' location (reflecting glances in the opposite direction to this individual's gaze), the 'central' location (a fixation on the model itself) or 'elsewhere'.

Coding was repeated in 15% of trials by an independent experimenter, with subsequent analysis conducted to determine inter-rater reliability amongst the two scorers. Reliability was found to be high with coders displaying considerable agreement

in their analysis of the location of subjects' inspections (Cohen's  $K = 0.74$ ).

### 2.5. Data analysis

The number of valid co-orientation trials conducted with the two subjects totalled 73, 36 with the female gibbon, Giava, and 37 with the male gibbon, Ipan. A considerable number of additional trials were discarded from the analysis, most commonly due to subjects becoming inattentive to the stimuli or distracted during the testing procedure. Of the 73 valid trials, the expectancy violation stage was possible on 48 occasions, with an equal number of congruent and incongruent trials conducted during this phase of the experiment.

### 2.6. Stage 1: visual co-orientation

The subjects' responses during the first stage of the trials were assessed to determine whether there was a tendency for tracking the visual orientation of the stimulus individual towards an external location prior to the appearance of an object. Analysis of performance in this first phase of the trials involved the examination of subjects' initial glances on presentation of the stimulus model and the duration of all inspections throughout this period. Measures of initial fixations were assessed for each subject by means of binomial tests comparing the number of glances directed to the target location as opposed to the anti-target region across trials.

In a direct replication of Scerif et al's (2004) design, trials were disregarded from the analysis of initial fixations where the first glance was directed towards the stimulus individual or to other regions of the screen. The decision to exclude first fixations on these areas follows the convention for research of this nature (e.g. Lorincz et al., 1999) and is based on two considerations. Specifically, it is reasoned that external interference or distractions may be the cause of glances to peripheral locations, whilst fixations on the stimulus individual may be due to the stimulus individual's status as a social being.

The duration of subjects' inspections in the first phase of the trials was also analysed to determine whether each individual preferentially directed their attention to the target location during this period. The average number of video frames per trial in which subjects' attended to both target and anti-target areas was thus assessed and compared using a Wilcoxon signed ranks test. All statistical tests were two-tailed.

### 2.7. Stage 2: expectancy violation

Subjects' reactions to compatible and incompatible sequences in stage two of the trials were analysed for evidence that they are capable of detecting anomalies in the relationship between an agent and an object. In accordance with Scerif et al. (2004) and Call et al's (1998) work we assessed whether subjects showed a tendency to re-inspect the stimulus individual in the event of finding a target object in a position that was inconsistent with this individual's gaze. Following similar reasoning to that used by Scerif et al. (2004), attributions of

checking behaviour were only made where subjects re-inspected the stimulus individual having previously located the target object in an unattended position. This stipulation was designed to ensure that subjects' fixations on the depicted individual in incompatible trials could not be attributable to their eye gaze arbitrarily falling on the nearest available stimulus following their failure to find an object of interest in this individual's gaze.

In the light of such reasoning, the experimenter coded subjects' first glances immediately subsequent to their discovery of the object as either 'stimulus individual' or 'elsewhere', and conducted a Chi-square analysis to compare such responses across compatible and incompatible trials. In addition the experimenter monitored the duration of subjects' gazes towards these two regions throughout the second stage of the trials. These measures were then assessed using a Mann-Whitney test. Once again the statistical tests were two-tailed.

## 3. Results

### 3.1. Stage 1: visual co-orientation

Initial analysis indicated that subjects responded in a comparable way when presented with stimulus individuals gazing to the left and to the right. No significant differences were found in the time spent inspecting target and anti-target positions when exposed to left and right facing images ( $t$ -tests:  $t = 0.616$ ,  $p = 0.542$ , for the male individual and  $t = 0.599$ ,  $p = 0.560$ , for the female, respectively). Trials involving left and right facing images were therefore amalgamated for further analysis.

Assessments of the subjects' initial inspections on presentation of a human model indicate that both individuals tended to direct their attention towards the target location significantly more often than the anti-target position (Binomial Test: Giava (16/4),  $p < 0.05$  and Ipan (11/3),  $p < 0.05$ , Fig. 2). Further analysis of the duration of subjects' gazes throughout stage 1 of the human trials reveals significant differences in the time spent looking towards each of these locations. Both subjects spent a greater proportion of time attending to the target area than the anti-target region, prior to the appearance of the stimulus object (Giava: Wilcoxon signed rank test,  $T = 46.07$ ,  $N = 20$ ,  $p < 0.05$ , Ipan: Wilcoxon signed rank test,  $T = 12.485$ ,  $N = 14$ ,  $p < 0.01$ , Fig. 3).

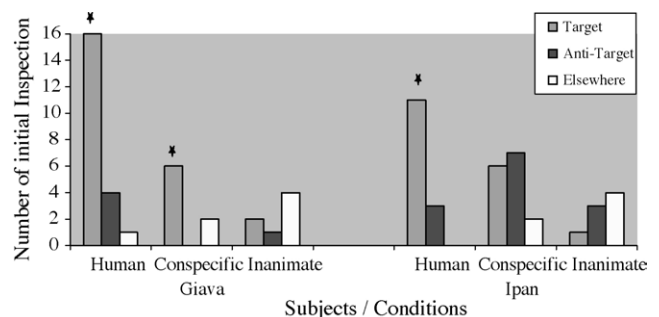


Fig. 2. Total number of trials in which first fixations were directed towards target, anti-target and other (elsewhere) locations. Star indicates  $p < 0.05$  for binomial test between target and anti-target.

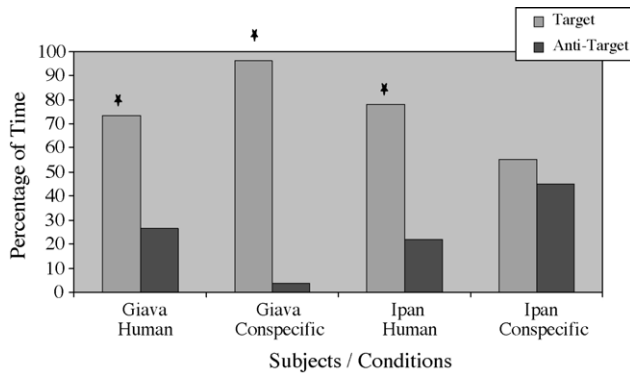


Fig. 3. Proportion of time spent inspecting the target and anti-target locations by each subject in the first stage of the trials. Star indicates  $p < 0.05$  for Wilcoxon ranked pairs test.

Findings relating to the female gibbon, Giava, reveal a similar pattern of results in response to a conspecific stimulus. Analysis indicates that this individual's initial glances were significantly more likely to be directed towards the target area than the anti-target area (Binomial Test: (6/0),  $p < 0.05$ , Fig. 2), and she also focused her attention on this location for a significantly greater proportion of time throughout the first phase of the conspecific trials (Wilcoxon signed rank test,  $T = 0.0019$ ,  $N = 6$ ,  $p < 0.05$ , Fig. 3).

Conversely analysis of the male gibbon's performance in the conspecific condition suggest that there was no significant difference in the number of initial inspections directed towards the target and anti-target regions, with 46.15% and 53.85% of glances aimed at each location, respectively (Binomial Test: (6/7),  $p = 1.0$ , Fig. 2). Furthermore, the duration of looks to each of these positions did not significantly differ throughout the stage 1 period, with the subject spending a similar proportion of time inspecting the two positions (Wilcoxon signed rank test,  $T = 40.406$ ,  $N = 13$ ,  $p = 0.754$ , Fig. 3).

Discrepancies in the male gibbon's performance with human and conspecific models are further consolidated by analysis comparing this subject's initial fixations in these two conditions. An assessment of this subject's tendency to direct first inspections towards the target area as opposed to all other regions indicates significant differences in the gibbon's responses across conditions, with human models eliciting a significantly greater number of looks to the target position than conspecific models (Chi-square test:  $\chi^2(1) = 4.438$ ,  $p < 0.05$ ). In contrast, a comparable analysis of the females performance in human and conspecific trials revealed no significant difference across these conditions (Chi-square test:  $\chi^2(1) = 0.0045$ ,  $p = 0.944$ ).

Finally analysis of both the gibbons' responses in the presence of an inanimate stimulus reveal that the subjects did not tend to direct their first gazes towards the target area. In fact we detected no significant difference in the subjects' inspections of target and anti-target locations (Fig. 2).

### 3.2. Stage 2: expectancy violation

An assessment of the female gibbon's initial inspections on discovery of the target object indicate that she was sig-

nificantly more likely to check back to the stimulus individual when the toy appeared in an incongruent position than when it appeared in a congruent location (Chi-square test:  $\chi^2(1) = 7.72$ ,  $p < 0.01$ ). Furthermore, an examination of the time spent inspecting the depicted model throughout the second phase of the trials revealed that this individual attended to the stimulus model for significantly longer when presented with incompatible sequences than when exposed to compatible trials (Mann–Whitney  $U$ -test:  $U = 39.0$ ,  $n_1 = 11$ ,  $n_2 = 15$ ,  $p < 0.01$ ).

The male gibbon also directed more of his initial gazes towards the stimulus individual in incongruent trials, compared with congruent. However, this was not significant (Chi-square test:  $\chi^2(1) = 2.764$ ,  $p = 0.097$ ). Nonetheless, the duration of this subject's inspections throughout the second period indicate that he looked back at the stimulus individual for a greater proportion of time when the object appeared in an incongruent position than when it appeared in a location that was consistent with the depicted individual's gaze (Mann–Whitney  $U$ -test:  $U = 24$ ,  $n_1 = 8$ ,  $n_2 = 14$ ,  $p < 0.05$ ).

Separate analyses concerning the subjects' behaviour in the human and conspecific conditions also revealed intriguing differences in their responses to these different models. Results relating to the female gibbon indicate that this subject attended to the conspecific for significantly longer when the object appeared in an incompatible position than when it appeared in a position that was consistent with this individual's gaze (Mann–Whitney  $U$ -test:  $U = 0.5$ ,  $n_1 = 4$ ,  $n_2 = 5$ ,  $p < 0.05$ , Fig. 4). However analysis of this subject's behaviour in response to the human model found no significant difference in the time spent inspecting this individual across congruent and incongruent trials (Mann–Whitney  $U$ -test:  $U = 25.5$ ,  $n_1 = 6$ ,  $n_2 = 11$ ,  $p = 0.475$ ).

Conversely an assessment of the male gibbon's behaviour in the human condition indicated that he attended to the stimulus model for significantly longer when the object appeared in an incompatible location than when it appeared in a position that was consistent with the agent's direction of gaze (Mann–Whitney  $U$ -test:  $U = 2.5$ ,  $n_1 = 5$ ,  $n_2 = 7$ ,  $p < 0.05$ , Fig. 4). However this individual did not show an equivalent performance in trials in which the stimulus individual was a conspecific. In this condition analysis reveals no significant differences in the gibbon's inspections across incongruent and congruent trials (Mann–Whitney  $U$ -test:  $U = 8.0$ ,  $n_1 = 3$ ,  $n_2 = 7$ ,  $p = 0.667$ , Fig. 4).

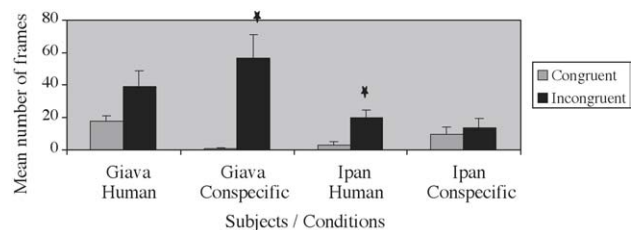


Fig. 4. Mean number of frames (+ standard error) in which subjects' inspected the stimulus individual in conspecific and human trials for congruent and incongruent conditions. Star indicates  $p < 0.05$  for Mann–Whitney test.

#### 4. Discussion

The experimental findings suggest a proficiency in the visual co-orientation abilities of the two gibbon subjects. Analyses of these individuals' responses reveal a reliable tendency for visual co-orientation, with both subjects consistently modifying their attentional focus to match the visual perspective of a human being. In contrast the subjects' responses to pictures of an inanimate model suggest that they were less inclined to exhibit attention-following behaviours, showing no significant tendency to look towards the target area throughout inanimate trials. These results seem to suggest that the gibbons assigned particular significance to the visual focus of animate beings and that their responses cannot be explained by an instinctive tendency for co-orientation with external objects.

Thus the study is consistent with the work of Myowa-Yamakoshi and Tomonaga (2001) in indicating that gibbons may be receptive to the direction of other individuals' visual orientation and capable of simple attention-following behaviour. Given the current paucity of gibbon research, these findings are extremely enlightening, allowing novel insights into the cognitive ability of a largely disregarded species.

A comparison of subjects' responses to human and conspecific models also reveals some interesting findings. Both subjects displayed a proclivity for co-orienting with humans, revealing that they were capable of both detecting and following the visual orientation of a species other than their own. Not unsurprisingly, the female gibbon exhibited a similar capacity for visual co-orientation in conspecific trials. Yet in contrast to expectations, the findings suggest that the male subject failed to show an equivalent tendency for attention following in response to a member of his own species.

These results seem to have some interesting implications. Given previously cited concerns about the use of human experimenters in attention-following studies it is significant that the subjects appeared to be skilful in detecting and interpreting the attentional cues of the human models. The study seems to be inconsistent with accounts that attribute past failures in such tests to difficulties in reading human visual cues. Instead the male gibbon showed a greater proclivity for co-orientation in human trials than when presented with a member of his own species, and for the current subjects the ability to identify human visual orientation seems to have been achieved with relative ease.

The male gibbon's heightened responsiveness to human models may however be considered surprising, particularly in view of previous studies testifying to the robustness of primates' gaze-following behaviour in studies with conspecifics (Tomasello et al., 1998; Emery et al., 1997). Furthermore, it is inconsistent with theoretical proposals suggesting animals may show a greater inclination for monitoring the visual gaze of their own species than other organisms (Povinelli, 1996; Itakura et al., 1999).

Of course these findings do not imply that this gibbon was incapable of visual co-orientation with conspecifics, and an explanation for this finding may be due to how the motivation to respond to different models developed in the course of his life history. Given previous suggestions regarding the importance of prior experience in individuals' responsiveness to different

species (Eddy et al., 1993), it is noteworthy that the zoo environment provided the subjects with a history of extensive contact with humans. The male subject's hand-rearing and prolonged period in captivity may have caused him to be particularly sensitive to the behaviour of humans. This consideration raises the possibility that the use of human models may still account for previous failures in attention-following studies, if these studies involved less enculturated sample populations.

To our knowledge a rigorous examination of how ontogenetic factors may affect such behaviour has not been conducted. However a number of studies have suggested that an individual's life history may be critical in shaping his later attention-following behaviour. Gomez (1996) has reported on differences in chimpanzees' responsiveness to a human's attentional state according to prior experience with this species. Whilst Call and Tomasello (1994) noted that enculturated orangutans appeared to be capable of sophisticated responses in an object choice paradigm, which their less enculturated counterparts seemed incapable of replicating. In the light of this finding, it seems that future research is needed to identify discrepancies in primates' responses to different species, and to determine the extent to which visual co-orientation is influenced by developmental factors.

In addition to providing evidence of simple visual co-orientation the current study also investigated more complex aspects of attention. Further analysis of the subjects' responses indicated significant differences in the behaviour of the gibbons in congruent and incongruent conditions, with both individuals' displaying a greater tendency for re-inspection when an object appeared in a position that was not in line with the depicted model's visual orientation. This kind of checking reaction has often been taken to indicate surprise and could suggest that the subjects were capable of detecting an incompatibility between visual orientation and the position of an object. Of course whilst this behaviour seems to exemplify a more sophisticated response than a simple, impulsive act of visual co-orientation, its interpretation remains open to question. In view of Gomez's (1996) suggestions regarding the overt nature of the mental process of attention, it is plausible that subjects may foster an appreciation of the relationship between visual orientation and the location of a target object, without making additional, more complex inferences about the attentional experiences of others.

The performance of the subjects in the current study may reflect an appreciation of attentional states that is distinct from both full mentalistic understanding and simple behavioural responding. Gomez (1996) provides support for such a possibility, writing that primates could possess some tacit appreciation of other individuals' mental states without being capable of explicit representations of such processes. Yet at present a firm conclusion remains elusive, and further research is needed to provide greater clarification of the mechanisms that underlie these more advanced attentional responses.

Analysis of the behaviour of the two subjects in the conspecific and human conditions suggested that they respond differently to these models. The female gibbon, Giava, exhibited a significant tendency for re-inspecting the stimulus individual in incongruent trials with the ape model, but showed no such tendency when presented with the human. Conversely the male

gibbon showed a significant tendency to look towards the stimulus individual in incongruent trials involving the human model, but no such difference in response to the conspecific.

The life history of these individuals could once again provide a possible explanation for variations in their response. The male gibbon's apparent sensitivity to violations in the relationship between a human's visual orientation and an object may have developed as a consequence of his human-rearing, whilst the less individualised nature of the female's contact with humans may explain her poorer performance in this condition. The current evidence thus calls for a more rigorous examination of how life history may affect such processes. Such an assessment could provide important insights, going some way to explain previous inconsistencies in the performance of primates across different studies.

In summary, the current research provides evidence that gibbons are proficient in following the attentional direction of others. Furthermore, the findings indicate that certain individuals (perhaps particularly those with a previous history of contact with humans) may show a tendency for visual co-orientation with both conspecific and human models. The study also supports the work of Scerif et al. (2004) in suggesting that, like Diana Monkeys, gibbons may possess some notion of how the direction of an individual's visual orientation relates to the position of an external object. In the light of this research, it appears that further investigation of how attention-monitoring behaviour may develop in the course of a primate's lifetime is a necessary and challenging prospect for future research.

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