

Reflexive Social Attention in Monkeys and Humans

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Summary

For humans, social cues often guide the focus of attention. Although many nonhuman primates, like humans, live in large, complex social groups, the extent to which human and nonhuman primates share fundamental mechanisms of social attention remains unexplored. Here, we show that, when viewing a rhesus macaque looking in a particular direction, both rhesus macaques and humans reflexively and covertly orient their attention in the same direction. Specifically, when performing a peripheral visual target detection task, viewing a monkey with either its eyes alone or with both its head and eyes averted to one side facilitated the detection of peripheral targets when they randomly appeared on the same side. Moreover, viewing images of a monkey with averted gaze evoked small but systematic shifts in eye position in the direction of gaze in the image. The similar magnitude and temporal dynamics of response facilitation and eye deviation in monkeys and humans suggest shared neural circuitry mediating social attention.

Results and Discussion

Where we look often betrays our intentions and desires. Not surprisingly, when we see a person looking in a particular direction, we reflexively and covertly orient our attention, as well as our overt gaze, in the same direction [1–4]. This gaze-following reflex is considered to be a precursor to more complex sociocognitive abilities in humans, such as theory of mind [5], and is compromised in neurodevelopmental disorders such as autism [6] and Turner syndrome [7]. Understanding the neural basis of gaze following and other aspects of socially mediated attention, as well as their disruption in neurological disorders, would be facilitated by an animal model. Although several studies have reported that some nonhuman primate species orient gaze overtly in the same direction as another individual [8–11], there is no evidence that nonhuman primates covertly shift attention where another individual is looking [12], and no study has directly compared social attention in humans and any animal species.

To investigate directly whether humans and monkeys exhibit similar sensitivity to where another individual is

looking, we asked humans and rhesus macaques to shift their gaze from a central stimulus to a peripheral target appearing randomly on the left or right following the presentation of an image of a rhesus macaque randomly looking to the left or right for 100, 200, 400, or 800 ms. A critical feature of this task is that the direction of gaze in the monkey face did not predict the location of the target. We presented two monkey face images in blocks: one of a rhesus macaque with its head oriented forward and its eyes averted to the left or right (“Eyes Only”) and a second of the same monkey with both its head and eyes averted to the left or right (“Head & Eyes”).

For both images, standardized reaction times for monkeys and humans were faster when the target appeared in the direction indicated by the monkey face (*Congruent Condition*), particularly when faces were viewed for 200 ms (Figure 1A). For both species, a $2 \times 2 \times 4$ ANOVA (congruency [congruent or incongruent] \times image [“Head & Eyes” or “Eyes Only”] \times viewing duration [100, 200, 400, or 800 ms]) indicated an interaction between viewing duration and congruency (monkey: $F = 4.78$, $df = 3,6240$, $p = 0.002$; human: $F = 4.45$, $df = 3,1648$, $p = 0.004$). Post-hoc t tests revealed that, for each species and for both images, standardized reaction times in congruent trials were significantly faster when faces were viewed for 200 ms (for humans, viewing the “Eyes Only” image for 800 ms also resulted in faster reaction times in congruent trials). Moreover, this result was consistent across subjects: at 200 ms, all subjects, with both images, exhibited faster standardized reaction times in congruent trials, and this effect was significant for one individual monkey subject and one individual human subject for each image. These data are consistent with the idea that viewing a face with its gaze oriented in a particular direction reflexively and covertly shifts attention in the same direction in both monkeys and humans.

Covertly orienting attention is often accompanied or followed by small but systematic eye movements in the same direction [13, 14], and the activation of brain areas involved in oculomotor processing is associated with spatial shifts of attention [15]. Such findings suggest a close relationship between spatial attention and eye movements. Although our subjects were required to maintain fixation within a small tolerance zone, we explored whether, in addition to improving reaction times for detecting peripheral targets, viewing a monkey looking in a particular direction was also associated with systematic changes in eye position. We found that, immediately before initiating a correct response, eye position within this tolerance zone was biased in the direction indicated by the monkey face, especially with longer viewing times (Figure 1B; $2 \times 2 \times 4$ ANOVA, interaction between viewing duration and gaze direction; monkey: $F = 8.36$, $df = 3,6240$, $p < 0.0001$; human: $F = 6.34$, $df = 3,1648$, $p < 0.001$). With 400 and 800 ms viewing durations, eye position was biased in the direction of gaze in the monkey face for all subjects viewing both images (with the exception of one monkey subject viewing the “Head & Eyes” image for 800 ms). Furthermore,

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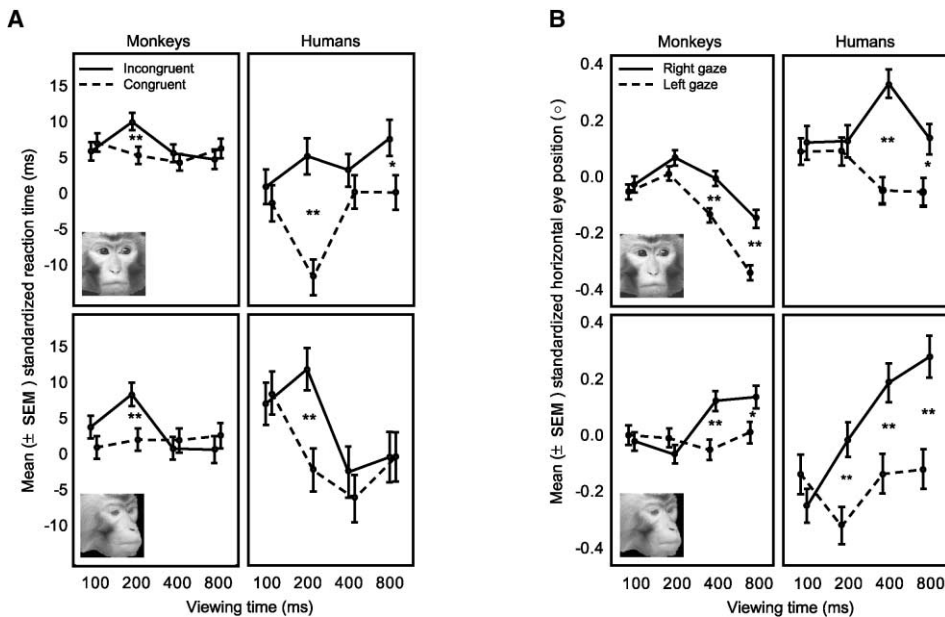


Figure 1. Effects of Social Cues on Reaction Time and Eye Position

(A) Mean (\pm SEM) standardized reaction times for congruent (dashed) and incongruent (solid) trials. Top row: “Eyes Only” image; bottom row: “Head & Eyes” image.

(B) Mean (\pm SEM) standardized horizontal eye position for rightward- (solid) and leftward (dashed)-gazing images. Post-hoc t test: * $p < 0.05$; ** $p < 0.001$.

these effects were statistically significant for two individual monkey subjects and two individual human subjects viewing the “Eyes Only” image for either 400 or 800 ms, and for three individual monkey subjects and one individual human subject viewing the “Head & Eyes” image for either 400 or 800 ms.

A crucial question is whether these changes in eye position within the tolerance window were produced, at least in part, by microsaccades, which are hypothesized to overtly indicate covert shifts of attention [13, 14]. To address this issue, we measured, for each trial, the first eye movement reaching a velocity of 8° s^{-1} and occurring after the onset of the gaze image but prior to the response to the target. Such eye movements were detected in 25% of trials for monkeys and 32% of trials for humans. The vast majority of these microsaccades occurred with the 400 and 800 ms viewing times (monkey: 96%; human: 97%). These movements exhibited a linear relationship between peak velocity and amplitude characteristic of saccades (monkey: $r^2 = 0.11$, $b = 30.3$, $df = 1,1568$, $p < 0.0001$; human: $r^2 = 0.28$, $b = 36.3$, $df = 1,528$, $p < 0.0001$) and were of small amplitudes, typical of microsaccades (monkey: $0.83^\circ \pm 0.2^\circ$; human: $0.86^\circ \pm 0.2^\circ$). Crucially, the horizontal amplitude of these microsaccades was biased by the direction of gaze in the monkey face. On average, rightward-gazing monkey faces evoked rightward microsaccades, and leftward-gazing monkey faces evoked leftward microsaccades, for both monkeys ($F = 18.91$, $df = 1,1566$, $p < 0.0001$) and humans ($F = 77.46$, $df = 1,528$, $p < 0.0001$). Together, our eye position and microsaccade results support the conclusion that both monkeys and humans reflexively and covertly orient attention in the direction in which another individual is looking.

An additional question is whether these shifts in the subjects’ eye position reflect holistic processing of the direction of gaze in the face or instead simply reflect a reorientation of gaze to the midpoint of the eyes in the image, which was slightly offset to one side or the other relative to the center of the image as well as the monitor. A previous investigation [4] demonstrated that, in humans, reflexive shifts of attention in response to faces with averted gaze cannot be fully explained by the spatial position of salient features. To address this issue in nonhuman primates, we collected additional data from two monkey subjects viewing a version of the “Eyes Only” image in which the midpoint of the two eyes was centered on both the image and the monitor rather than offset by 0.08° , as in the original image. We found that eye position within the tolerance window deviated in the direction of gaze in this image, and this effect became more pronounced with prolonged viewing ($F = 3.84$, $df = 3,1520$, $p < 0.01$; at 800 ms, post-hoc t test, $p < 0.001$). In addition, in trials in which microsaccades were detected, horizontal amplitude was biased by the direction of gaze in this modified image ($F = 2.72$, $df = 1,128$, $p = 0.02$). These data suggest that covert attention follows the direction of gaze in a viewed face, rather than the relative spatial positions of salient features.

The finding that social cues influence eye position raises the possibility that improved response times in congruent trials could be due to cortical magnification of visual stimulation nearer the retinal fovea as the line of sight deviates toward the target. In fact, one might argue that if small shifts in eye position within the fixation window could account for reaction time differences, then the shifts of attention evoked by gaze cues in our study, and previous ones [2–4], are better described as

overt rather than covert. To explore this issue, we tested whether the horizontal distance from the line of sight to the target, as estimated from eye position, predicted standardized reaction times when faces were viewed for 200 ms. We found that eye position did not predict reaction times for monkeys ($F = 1.13$, $df = 1,1454$, $p = 0.29$) but did so for humans ($F = 16.01$, $df = 1,389$, $p < 0.001$). When the influence of eye position was removed statistically, however, reaction times for human subjects were still significantly faster when peripheral targets appeared on the side indicated by the monkey face (ANCOVA; $F_{\text{face orientation}} = 22.12$, $df = 1,388$, $p < 0.0001$). Thus, faster reaction times in congruent trials likely reflect central changes in perceptual processing rather than movement-induced changes in retinal stimulation.

Under natural conditions, shifting attention to a peripheral visual stimulus is often followed by an overt reorientation of gaze to the same location. Although our task required subjects to maintain fixation on the monkey face prior to the appearance of the peripheral target, in some trials, subjects prematurely shifted gaze out of the fixation tolerance zone before the target appeared, despite the fact that such responses were incorrect (and monkey subjects were not rewarded for them). These erroneous saccades were generally in the direction indicated by the monkey face (173 of 259 errors for monkeys, binomial probability < 0.0001 ; 14 of 22 errors for humans, binomial probability = 0.14) and occurred almost exclusively in trials with 400 or 800 ms face viewing times (monkey: 98%; human: 100%). Combined with our previous analyses of response time, eye position, and microsaccades, these results suggest that, for both monkeys and humans, viewing a face looking in a particular direction reflexively and covertly shifts visual attention in the same direction and sometimes leads to an overt reorientation of gaze.

One intriguing aspect of our reaction time and eye position results is that the “Eyes Only” image produced effects as strong as those evoked by the “Head & Eyes” image (reaction times: both species, $p > 0.08$ for interactions of image \times congruency and image \times congruency \times viewing duration; eye position: both species, $p > 0.13$ for interactions of image \times gaze direction and image \times gaze direction \times viewing duration). Although previous studies have shown that humans are sensitive to both types of cues [2–4, 16], prior studies with nonhuman primates have been equivocal [8, 11, 12, 17–19]. Those studies, along with the demonstration that the eyes of nonhuman primates are characterized by a low contrast border between the iris and conjunctiva [20], have led to the suggestion that nonhuman primates may be unable to use the eyes as a sole indicator of gaze direction [12, 21]. Our data, however, demonstrate that the eyes of rhesus macaques carry ample information for other primates to determine their gaze direction. Previous studies reporting a lack of overt orienting by nonhuman primates in response to viewing frontally oriented faces with averted eyes may have overlooked subtle and transient changes in covert attention revealed by precise spatial and temporal measurement of eye position in our study.

It is also notable that human subjects reflexively and covertly shifted their attention in the direction of gaze

in nonhuman primate faces. Reaction time differences between congruent and incongruent trials in our study were similar to those reported previously for human subjects performing target detection tasks while viewing human [3, 4] or schematic [2] faces with averted gaze. The question of whether nonhuman primates covertly shift their attention to where another human is looking has not yet been investigated; however, previous studies [8, 11] have demonstrated that nonhuman primates do overtly orient their attention in the direction of a human’s gaze. Collectively, these findings suggest that the perceptual channels responsible for detecting faces and their direction of gaze are broadly tuned in both monkeys and humans.

In nonsocial attention tasks, response times are facilitated when peripheral cue onset precedes the unpredictable onset of a target at the same location by roughly 100–200 ms but are inhibited with longer cue-target delays; these findings suggest a transient, reflexive, and covert shift of attention toward the cue [22, 23]. Unlike such exogenous orienting of attention, endogenous orienting of attention following the presentation of nonsocial symbolic cues at fixation results in response time facilitation for congruent targets at longer cue-target delays but no inhibition. Intriguingly, the response times of both our monkey and human subjects, like those reported for humans in similar prior studies [2–4], exhibited aspects of both exogenous and endogenous cuing of attention. Response times were facilitated when targets appeared in the direction of gaze in the face image after short viewing times but showed no inhibition after longer viewing times. Moreover, both our monkey and human subjects made microsaccades in the direction of gaze in the monkey face only after prolonged viewing. These data suggest that shifts of attention triggered by viewing a face with averted gaze may access a specialized social-orienting mechanism exhibiting aspects of both exogenously and endogenously cued attention [4].

Our results suggest that common mechanisms mediate fundamental processes of social attention in monkeys and humans. Recent neuroimaging studies in humans collectively implicate brain regions near the superior temporal sulcus in decoding where another individual is looking and the parietal cortex for orienting attention and gaze in the same direction [24]. Neuronal recording and ablation studies in monkeys have suggested that the superior temporal sulcus region may also be important for detecting gaze direction in faces [25, 26], but the role of parietal cortex in social attention remains unexplored in nonhuman primates. Our results raise the possibility that connections between neural circuits in temporal and parietal cortex may have evolved as part of a specialized module for controlling attention in both human and nonhuman primates living within complex societies.

Experimental Procedures

Subjects

Three adult male rhesus macaques participated in both experimental blocks. Monkeys were housed in pairs at the Duke University Medical Center Vivarium. All animal procedures were approved by the Duke University Medical Center Institutional Animal Care and Use Committee and were designed and conducted in compliance

with guidelines provided by the Public Health Service's Guide for the Care and Use of Animals.

Four adult humans, two male and two female, participated in the experiments (including the first author). The two males participated in both experimental blocks, whereas the two females participated in one block each. None of the humans had previous experience with this type of task, although two of the humans in each experiment were aware of the hypothesis under test. All human procedures were approved by the Duke University Medical Center Institutional Review Board.

Procedures

The experiments were run on a Dell Precision 220 Pentium IV computer, by using custom software (ryklinsoftware.com). Monkeys viewed stimuli on a 24" Sony Trinitron monitor running at a resolution of 1024×768 and a refresh rate of 60 Hz; humans viewed stimuli on a 16" LCD monitor at the same resolution and refresh rate. Subjects were seated with their eyes 45 cm from the center of the monitor.

For each experiment, one photograph was used to create both right- and left-oriented gaze images by using Adobe Photoshop. In the "Eyes Only" image, the gaze in the original photograph was oriented rightward, and the photograph was reflected horizontally to obtain the leftward gaze image; for the "Head & Eyes" image, the gaze in the original photograph was oriented leftward, and the rightward gaze image was generated by reflection. Face images were standardized by cropping the face from the background, resizing to 115×115 pixels, and then adjusting the mean luminance to match a neutral gray stimulus of the same size. To control for the possibility that the spatial offset of salient features such as the eyes in these stimuli might evoke orienting, we conducted a control experiment in which the original "Eyes Only" image was shifted so that the midpoint of the irises in the image was centered on the monitor and the sides of the image were cropped so the center of the image was also centered on the monitor. During experiments, all stimuli were presented on a dark background.

We used the magnetic search coil technique to monitor eye position [27, 28]. For monkeys, coils were surgically implanted beneath the conjunctiva monocularly; for humans, coils were embedded in a silicon rubber annulus (Skalar Medical) and, prior to each session, placed directly upon one eye. Monkeys' heads were held in place via a surgically implanted head restraint device (Crist Instruments). Human heads were held stationary with a chin rest. Eye position was sampled at 500 Hz. All surgical procedures followed standard techniques described previously [29].

In each trial, a subject fixated ($\pm 2^\circ$) a centrally placed, yellow square (subtending 3°) for 300–500 ms and maintained fixation ($\pm 2^\circ$) when the yellow square was replaced by a centrally placed face image or gray square (subtending 5°) for 100, 200, 400, or 800 ms. The face image or gray square was then extinguished, and a yellow square target simultaneously appeared 15° to the left or right. Subjects were required to shift their gaze, within 400 ms, to the indicated target area ($\pm 2^\circ$). We presented a gray square, rather than a face, in 1/3 of the trials to allow data to be standardized (see below) and pooled. Upon completing a trial successfully, a subject heard a 300 ms white-noise burst. Monkey subjects also received a liquid reward. If a trial was performed correctly, another trial followed after a 1- to 2-s intertrial interval (ITI). If a trial was performed incorrectly, another trial followed after a 3- to 4-s ITI. Humans were given breaks of 1–5 min if they requested one; monkeys were given breaks if they performed three consecutive trials incorrectly. Monkey subjects performed 700–1600 trials per session (mean = 1083 trials). Humans performed 300–700 trials per session (mean = 526 trials). Monkey subjects generally completed two sessions per experiment (mean = 1.83 sessions), whereas humans usually completed one (mean = 1.16 sessions). Humans performed fewer trials because the search coil annulus is not recommended to be worn for longer than 40 min [30].

We defined the onset and offset of task-related saccadic eye movements by using an acceleration criterion. Microsaccades were defined by using an acceleration criterion with a lower threshold (onset, 8° s^{-1} for three consecutive 2-ms samples; offset, 5° s^{-1} for one sample). Prior to statistical tests, reaction time and horizontal

eye position values were standardized relative to performance with the gray stimulus by computing, for each subject in each session and for each viewing time, the mean reaction time and horizontal eye position and then subtracting these values from the values obtained in trials in which a face image was displayed. Only correct trials were used for analysis of reaction time, eye position, and microsaccades.

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