

Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*)

Stephen V. Shepherd · Michael L. Platt

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Abstract Both human and nonhuman primates preferentially orient toward other individuals and follow gaze in controlled environments. Precisely where any animal looks during natural behavior, however, remains unknown. We used a novel telemetric gaze-tracking system to record orienting behavior of ringtailed lemurs (*Lemur catta*) interacting with a naturalistic environment. We here provide the first evidence that ringtailed lemurs, group-living prosimian primates, preferentially gaze towards other individuals and, moreover, follow other lemurs' gaze while freely moving and interacting in naturalistic social and ecological environments. Our results support the hypothesis that stem primates were capable of orienting toward and following the attention of other individuals. Such abilities may have enabled the evolution of more complex social behavior and cognition, including theory of mind and language, which require spontaneous attention sharing. This is the first study to use telemetric eye-tracking to quantitatively monitor gaze in any nonhuman animal during locomotion, feeding, and social interaction. Moreover, this is the first

demonstration of gaze following by a prosimian primate and the first to report gaze following during spontaneous interaction in naturalistic social environments.

Introduction

Over the last decade, much emphasis has been placed on the ability to recognize and respond to the orienting behavior of others (e.g. Baron-Cohen 1994). Such visual acquisition of social information would seem to depend on an initial bias to attend to others, in particular to the orientation of bodies, heads, and eyes (Kaminski et al. 2004). Both human and nonhuman primates preferentially gaze toward other individuals, in particular their faces and eyes, under laboratory conditions (Butler 1954; Sackett 1966; Haude and Ray 1974; Deaner et al. 2005). Furthermore, the ability to use social cues such as gaze direction (reviewed Emery 2000; Itakura 2004) has been reported not only in primates, but in species as diverse as dolphins (Tschudin et al. 2001), goats (Kaminski et al. 2005), and ravens (Bugnyar et al. 2004).

One caveat in interpreting such findings is that different measurement techniques and social contexts can themselves influence gaze-following behavior. For example, controlled studies of humans performing artificial “social” tasks report few deficits in gaze following by autistic individuals (Chawarska et al. 2003; Swettenham et al. 2003; but see also Ristic et al. 2005) despite severe disruptions of shared attention outside the laboratory (APA 1994). Complicating matters further, gaze following in typically developing humans is influenced by both gender (Bayliss et al. 2005; Deaner et al. 2007) and familiarity (Deaner et al. 2007). Even the term “gaze following” has been used to indicate a number of different social orienting behaviors

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S. V. Shepherd (✉) · M. L. Platt
Department of Neurobiology,
Duke University Medical Center,
Durham, NC 27710, USA
e-mail: svsv@duke.edu

M. L. Platt
Center for Cognitive Neuroscience,
Duke University, Durham, NC 27710, USA

M. L. Platt
Department of Biological Anthropology and Anatomy,
Duke University Medical Center, Durham, NC 27710, USA

(see Emery 2000 for discussion). In this document, we use “gaze following” to indicate an increase in gaze-alignment between the subject and animals in his field of view, specifically one that follows overt orienting to that animal.

Social context also shapes social attention in nonhuman animals. For example, gaze following in rhesus macaques is influenced by the social status of both the subject and the observed animal (Shepherd et al. 2006). Although several animal species have been reported to use social orienting cues in experimental contexts, such conditions may fail to include important variables that influence deployment of attention under more natural conditions. In particular, most studies of gaze following in animals have used human experimenters as attention cues—a decidedly non-naturalistic source of social information.

These methodological and contextual considerations suggest that quantifying how gaze is spontaneously deployed during natural social behavior would be crucial for understanding the evolution, development, and neurobiology of gaze following. Yet, where animals look during natural behavior remains virtually unknown (though note Land and Hayhoe 2001; Carmi and Itti 2006 for work with humans). Here we probe spontaneous social orienting behavior in ringtailed lemurs (*Lemur catta*) during ongoing behavior in relatively rich physical and social contexts. Ringtailed lemurs form mixed-sex aggregations of 10–20 individuals organized into well-defined social hierarchies, and communicate through auditory, olfactory, and visual modalities (Jolly 1966; Sauther et al. 1999). Previous studies (Itakura 1996; Anderson and Mitchell 1999) reported that ringtailed lemurs do not follow human gaze in experimental contexts. Our study differs from these studies, first and foremost, in that we examine responses to animal, rather than human, gaze cues (Tomasello et al. 1998). Additionally, this study is unique in using telemetric infrared video eye-tracking technology to increase the precision and sensitivity of measurements (Shepherd and Platt 2006), and in focusing on spontaneous instances of social orient-

ing in order to achieve a species-typical balance of competitive and cooperative motivations (see Hare and Tomasello 2004). In this study, we specifically quantified each lemur’s pattern of fixation near lemurs and other potentially salient objects (e.g., food rewards and high-contrast environmental features), and relative to the directions of observed lemurs’ head and body axes.

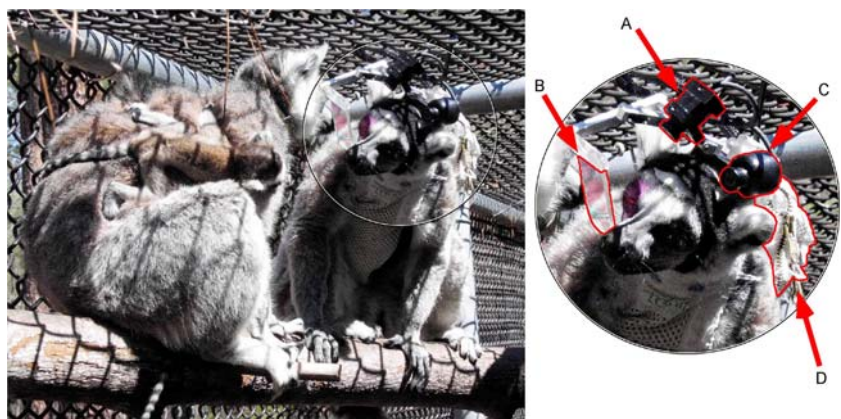
Methods

We recorded gaze position in two adult male ringtailed lemurs using a wireless infrared optical gaze-tracking system (see Shepherd and Platt 2006 for detailed methods). We worked exclusively with males to avoid complications from pregnancy and nursing during training and experimental sessions. System weight was approximately one-fourth of subjects’ mass, similar to that experienced by females carrying twins, and did not preclude a normal range of locomotion and social interaction (see Fig. 1). Recordings were made during terrestrial and arboreal locomotion, leaps, foraging, and social interaction.

Gaze tracking was accomplished using a wireless dual-camera system. One camera recorded eye position using infrared light, while the other captured the scene visible forward from the subject’s head. A five-point calibration procedure linked recorded eye positions to the corresponding visual stimuli in the scene camera. Signal transmission was vulnerable to several types of distortion or interruption, and while data was collected at 60 Hz, a 200 ms smoothing window precluded neat segmentation of gaze data into fixation, pursuit, and saccade. For digital annotation and analysis, data was downsampled to 30 Hz.

Subjects habituated gradually to gaze tracking after 4–6 weeks of thrice-weekly 1-h sessions. Cohabitant lemurs showed no obvious behavioral changes in response to the recording equipment. Human experimenters periodically gave the lemurs food during recordings to maintain activ-

Fig. 1 Gaze-tracking set-up. Gaze-tracking hardware consisted of an infrared LED and camera (a) monitoring the eye by dichroic mirror (b), a head-mounted scene camera (c), and a wireless transmitter housed in a primate backpack (d)



ity levels. Subjects were studied in their respective home habitats. Lemur “Licinius” was housed in three connecting outdoor rooms ($1.4 \times 2.0 \times 3.4$ m each) with branches, potential food sources, platforms, and another lemur (“Maurice”, a brown lemur, *Eulemur fulvus*). Lemur “Aracus” was housed in two indoor ($1.8 \times 1.6 \times 2.4$ m each) and one outdoor ($3.7 \times 3.9 \times 2.4$ m) connected enclosures; recordings from Aracus were also taken in another outdoor enclosure with similar dimensions and in a large, unroofed, treeless pen (5.6×85 m). Aracus shared these areas with up to 12 lemurs: 3 adult females, 4 juveniles, 4 infants, and 1 older male. The environments occupied by Licinius (one adult male heterospecific lemur companion) and Aracus (3 adult female and up to 1 adult male and 9 juvenile conspecifics) were distinct, and behavior was unconstrained rather than experimentally controlled. As experimental conditions varied substantially, but not systematically, across sessions and subjects, these data were collapsed prior to analysis.

Video data were gathered from five 1-h recording sessions (2 in Licinius and 3 in Aracus) and digitized at $0.22^\circ \times 33$ ms resolution. One-minute excerpts, chosen for optimal signal strength, were selected for manual coding. These clips were manually coded in a custom-designed Matlab environment (Skriatok Videoscore, <http://www.duke.edu/~svs/skriatok>) to note whether the subject was moving or stationary and to extract the frame-by-frame visual coordinates of the subject’s gaze and of four categories of regions of interest (ROI). Categories of ROI were selected *a priori* based on putative reward value, locomotor relevance, or social relevance: in general, markers were placed at specific positions on all visible humans (H), lemurs (L), food rewards (F), and at a small number of centrally-located, high-contrast environmental features (E). The end result of this coding was a marked video sequence from which we could derive gaze scanpaths, head-centered eye position, and the proximity of gaze to the various categories of ROI. When possible, lemurs were specifically marked at positions including the snout, eyes, body center, and tailbase. Observed head and body orientation were extracted from ROI based on the vector pointing from the tailbase toward the head and from the eyes toward the snout, respectively. See supplemental material for an annotated video sample. In total, 76 min of video were coded for analysis: 15 clips with lemur Licinius and 61 clips with lemur Aracus. For co-orienting analyses, 10 clips (all from Aracus) that were found to track gaze onscreen on fewer than half their samples were discarded. We operationalized fixation as any instances in which gaze fell within 10° of an ROI, a distance chosen to accommodate the 4° width of lemur fovea (Pariante 1975)/area centralis (von Rohen and Castenholz 1967) as well as smoothing artifact and drift in gaze calibration.

Because lemurs moved freely through a naturalistic environment, different regions and vectors of interest had different chance likelihood of being a given distance from fixation. For example, if the lemur primarily stayed in a room with three lemurs on screen but only one food reward, the other lemurs would be more likely to appear close to fixation by simple coincidence. For these reasons we constructed a baseline “chance” distribution using a time-shuffled bootstrap. To do this, we randomly paired gaze and ROI coordinates from different time samples within each clip. These pairings were repeated 200,000 times for linear measures and 100,000 times per animal for angular measures. The distribution of linear and angular statistics generated the “chance” distance and offset expectations predicted by the null hypothesis that the lemur *ignored* these regions or directions of interest when allocating visual attention. This time-shuffling procedure thus allowed us to control for irregularities in gaze-tracker calibration or statistical accidents in the number and distribution of ROI extracted from different clips and sessions.

Bootstrapping procedures were applied as follows: We first calculated the parameter of interest, for example “the portion of time lemurs were within 10° of gaze”. We next repeated this calculation 10,000 times, using an equivalent number of samples, but this time drawing from time-shuffled data instead of raw observations. We accepted as significant any observed parameters that were among the lowest or highest 250 time-shuffled values (two-tailed permutation test, alpha $P = 0.05$; see Hesterberg et al. 2005). Exact P values can be calculated by multiplying the number of outliers by $2/10,000$: with 10,000 repetitions, $P < 0.0002$ cannot be distinguished from 0. This procedure is easily adapted to assess other parameters, for example “portion of time by which environmental features were fixated less during rest than locomotion, less the portion of time by which lemurs were fixated less during rest than locomotion.”)

In addition to these bootstrap procedures, we also analyzed the temporal sequence of gaze vectors around fixation events, determining the dispersion (angular variability, see Fisher 1993) of gaze vectors and the shared-hemifield frequency (χ^2 test) before and after subject lemurs aligned their gaze with the observed individuals.

Please see supplemental video S1 for a brief sample of annotated data. More sample videos are available at <http://www.duke.edu/~svs/research/lemurgaze>.

Results

We first report that ringtailed lemurs showed a bias to fixate near other lemurs. In Fig. 2 we show fixations within 10° of humans, lemurs, food rewards, and stationary environmental features relative to chance. Across 76 min of

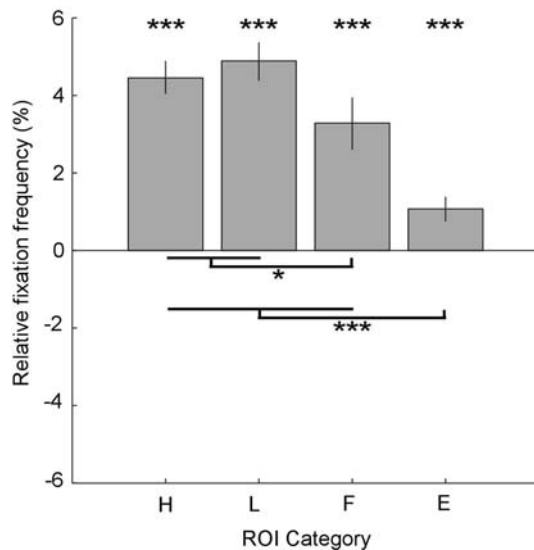


Fig. 2 Lemurs are biased to look towards other lemurs. Gaze bias was computed by examining the portion of observations in which the subject lemur looked within 10° of the nearest member of a category of interest; from these values we subtracted a time-shuffled baseline in which 10,000 bootstrap estimates were calculated from randomly paired gaze and scene coordinates. Categories include humans (*H*), lemurs (*L*), food rewards (*F*), and environmental features (*E*). Gaze bias, as plotted here, indicates the amount by which overt visual orienting toward key regions of interest exceeded chance expectation. Bars reflect the 95% confidence interval derived from the time-shuffled bootstrap procedure (see [Methods](#)). Three stars indicate $P < 0.0005$; two, $P < 0.001$; one, $P < 0.01$

data, we found that lemurs consistently biased their gaze toward all measured ROIs—humans (36,739 samples, permutation test, $P < 0.0002$), lemurs (26,543 samples, permutation test, $P < 0.0002$), food rewards (11,344 samples, permutation test, $P < 0.0002$), and high-contrast environmental features (53,735 samples, permutation test, $P < 0.0002$)—but fixations toward animate stimuli were more common than those toward food rewards (vs. humans, permutation test, $P = 0.004$; vs. lemurs, permutation test, $P < 0.0002$), and both animate stimuli and food rewards were more fixated than static environmental features (vs. humans, or lemurs, or food rewards, permutation test, $P < 0.0002$). Lemurs and humans were fixated with equal frequency (permutation test, $P = 0.2034$). Though the saliency of humans in this experiment may have derived from methodological constraints (e.g., capture to manipulate recording equipment and food provisioning to maintain activity levels), the saliency of lemurs likely reflected the intrinsic value of orienting toward these stimuli during natural behavior.

We next analyzed epochs in which lemurs either were moving between locations or were stationary (Fig. 3). During movement epochs, attention to humans (1,242 movement and 32,620 stationary samples, permutation test,

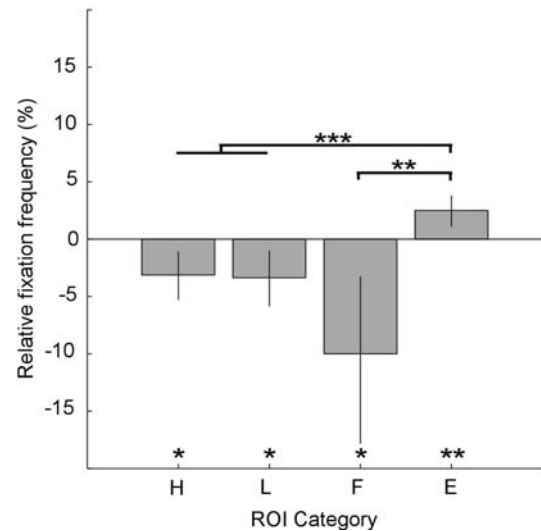
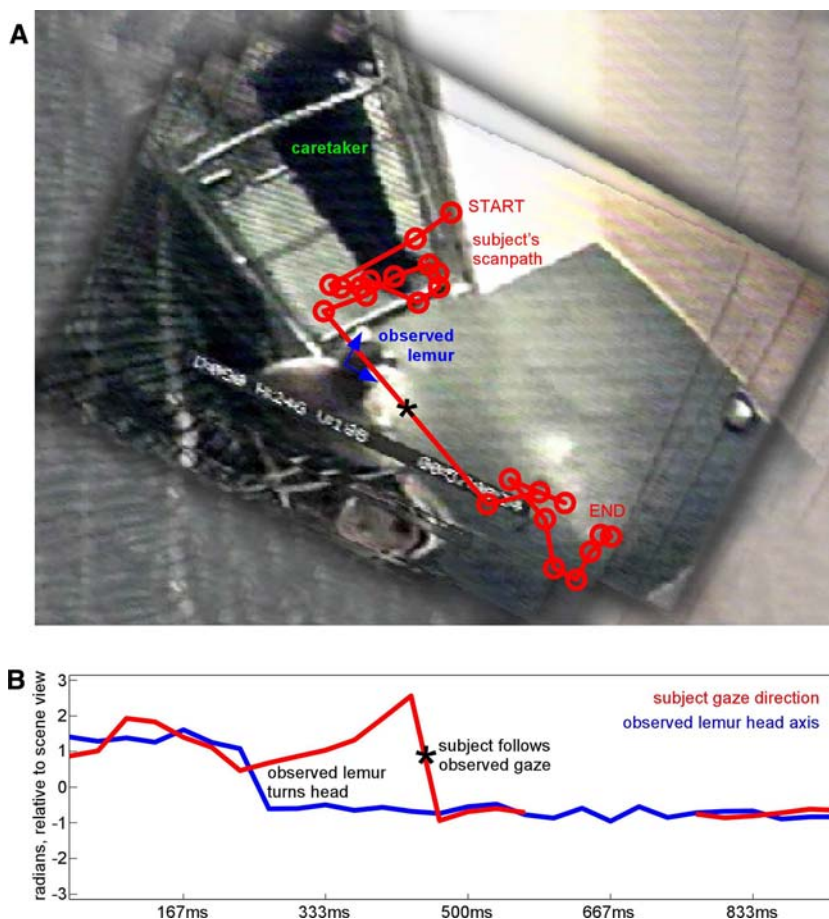


Fig. 3 Lemur orienting priorities shift during locomotion. Attention to humans (*H*), lemurs (*L*), and food (*F*) is reduced, with a concomitant increase in attention to high-contrast environmental features (*E*) along the path of transit. Gaze bias was calculated as per Fig. 2, with positive values indicating categories fixated more often during movement than during rest. Bars reflect the 95% confidence interval derived from the time-shuffled bootstrap procedure (see [Methods](#)). Three stars indicate $P < 0.0005$; two, $P < 0.001$; one, $P < 0.01$

$P = 0.0022$), lemurs (964 and 22,726 samples, permutation test, $P = 0.0042$), and especially food rewards (100 and 11,160 samples, permutation test, $P = 0.0024$) was reduced, but attention to environmental features (1,856 and 42,768 samples, permutation test, $P = 0.0006$) was increased (location priority change vs. human priority change, permutation test, $P < 0.0002$; vs. lemur, permutation test, $P = 0.0002$; vs. food, permutation test, $P = 0.0004$). These data demonstrate that context strongly influences where lemurs look. When stationary, they tend to monitor food sources, other lemurs, and humans. When moving, however, they ignore these stimuli and gaze along the path of their movement.

Given this strong bias to attend other lemurs, we next investigated whether this attraction may extend in the direction forward from their body and head axes. To test this idea, we examined the distribution of angular offsets between the subject lemurs' gaze direction and the observed lemurs' gaze directions. It is likely that humans use a combination of body, head, and eye cues to determine the direction another individual attends (Langton et al. 2000). Since lemurs have relatively low visual acuity (Kay and Kirk 2000), it seems unlikely that they use observed eye direction as the primary social attention signal. Therefore, we tested both the observed body and head axes as indices of observed gaze direction. We observed multiple instances in which both Licinius and Aracus appeared to follow another lemur's orienting behavior. For example, in Fig. 4 Aracus aligned gaze with a conspecific. When the

Fig. 4 An example of gaze following in ringtailed lemurs. **a** An observed lemur, recorded by the head camera across multiple frames, with the scanpath of the subject lemur superimposed in red. In this time period both observed and subject lemurs inspected the feet of a caretaker (“START”), then shifted gaze (*starred*) toward a proximal location on the floor (“END”). Blue lines represent the initial and final head axis of the observed lemur, here pictured mid gaze-shift. **b** Time-course of gaze following. Gaze angle plotted for the observed (*blue*) and subject (*red*) lemurs. The subject lemur traced a similar pattern to the observed lemur, but delayed in time. Furthermore, the subject lemur shifted his gaze to match the observed lemur’s heading (*starred*) only after fixating near to her



observed lemur turned her head, the subject looked toward her and followed her gaze. Across 66 min of video, we found that subject lemurs significantly concentrated their gaze (Fig. 5) with respect to observed lemurs’ head (200,975 samples; dispersion decreased 22%, permutation test, $P < 0.0002$; mean offset decreased 0.0232 radians, permutation test, n.s., $P = 0.0626$) and body axes (701,714 samples; dispersion decreased 77%, permutation test, $P < 0.0002$; mean offset decreased 0.0609 radians; permutation test, $P < 0.0002$).

These data suggest that lemurs orient their gaze in the same general direction as other lemurs in their field of view. There are two possible explanations for this gaze alignment. First, both lemurs independently shift their gaze in the direction of an external event. Second, the subject lemur actively follows the gaze of the observed lemur. If the observed gaze alignment reflects shared, but essentially independent, interests in environmental features and events, then gaze alignment should be similar before and after a subject shifts gaze toward an observed lemur. In contrast, if social gaze following is responsible for the observed co-orienting, then relative gaze alignment should increase immediately after a subject looks toward an observed lemur. To address this question, we examined the

time course of gaze alignment when the subject lemur shifted gaze to a lemur in view. We found a significant increase in gaze alignment with the observed head axis (1-0.5 second prior, $\chi^2 P = 0.52709$; 0.5-0 prior second, $P = 0.25135$; during fixation, $P = 0.011617$; 0-0.5 second after, $P = 0.011617$; 0.5-1 second after, $\chi^2 P = 0.020921$; details in legend of Fig. 6), but not body axis, immediately after Licinius or Aracus shifted gaze to an observed lemur (Fig. 6). These results demonstrate that lemurs tend to preferentially follow the gaze of individuals toward which they have just looked.

Discussion

Contrary to previous reports, our data demonstrate that *Lemur catta* use social cues to orient their attention during social interactions and often follow the gaze of other lemurs with their own. It has been previously reported that ~~ring-tailed~~ lemurs do not follow human gaze (Itakura 1996; Anderson and Mitchell 1999). Moreover, since prosimian visual acuity is lower than in other primates, it has been suggested that they instead rely nearly exclusively on olfaction (Brothers 1990; Sauther et al. 1999; Kay and Kirk

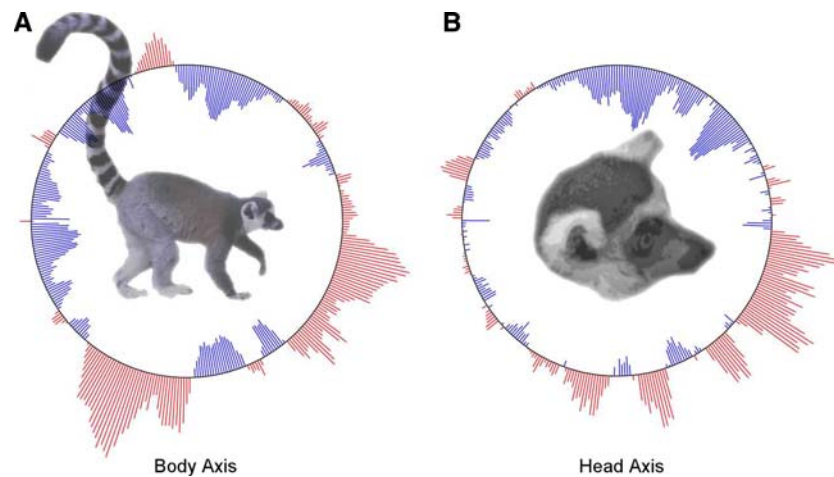


Fig. 5 Co-orienting in ringtailed lemurs. The graphs plot gaze alignment between the subject lemurs and observed lemurs across all video frames. Circular histograms plot the frequency with which a given angular offset was observed between the subject's fixation and the observed lemur's body (a) and head (b) orientation, relative to a time-shuffled baseline. Angular offsets were normalized, through reflection and rotation, so that rightward bars indicate perfect gaze alignment; leftward, perfect gaze avoidance; and upward/downward, approximately skyward/groundward deviations from the observed lemur axis.

Each line represents the number of observed instances of a given gaze deviation less the number expected based on a time-shuffled baseline: red outward-directed lines represent gaze relationships that are more often observed than expected, while blue inward-directed lines represents gaze relationships that are observed less often than would be expected due to chance. The largest amount by which observations exceeded expectation (i.e., the longest red line) is 0.17% per bin for body axis (a) and 0.14% per bin for head axis (b); there were approximately 57 bins per radian offset

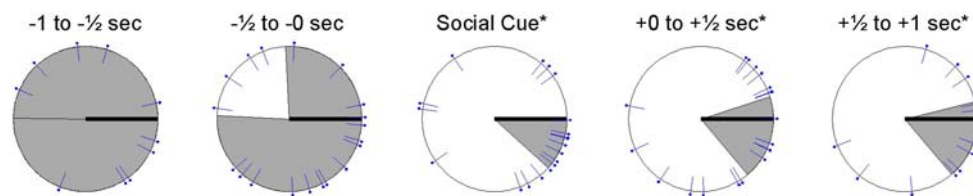


Fig. 6 Temporal dynamics of gaze-alignment suggest lemurs actively follow gaze. Successive panels show gaze alignment immediately before, during, and after subjects' gaze passed within 10° distance of the observed lemur (head and body loci only, tail ignored). Blue ticks mark individual observations (not all instances of fixation are represented in a given panel due to transient interruptions of the data stream). Shaded regions represent the mean gaze offset \pm the dispersion of the dataset (see Fisher 1993 for details), normalized so that the largest illustrated dispersion results in a fully shaded circle. We found a significant increase in gaze alignment with the observed head axis (1-0.5 second prior, 10 cases, dispersion 10.746, $\chi^2 P = 0.52709$; 0.5-0 prior second, 19

cases, dispersion 8.2311, $\chi^2 P = 0.25135$; during fixation event, 19 cases, dispersion 1.2252, $\chi^2 P = 0.011617$; 0-0.5 second after, 19 cases, dispersion 2.0248, $\chi^2 P = 0.011617$; 0.5-1 second after, 12 cases, dispersion 1.8942, $\chi^2 P = 0.020921$), but not body axis (1-0.5 second prior, 57 cases, dispersion 96.109, $\chi^2 P = 0.6911$; 0.5-0 prior second, 86 cases, dispersion 6421.4, $\chi^2 P = 0.82925$; during fixation event, 86 cases, dispersion 34.449, $\chi^2 P = 0.28089$; 0-0.5 second after, 86 cases, dispersion 87.623, $\chi^2 P = 0.51763$; 0.5-1 second after, 63 cases, dispersion 30.18, $\chi^2 P = 0.25684$), immediately after Licinius or Aracus shifted gaze to an observed lemur. Starred intervals are significantly aligned with gaze (χ^2 test $P < 0.05$)

2000; Gilad et al. 2004). In contrast, our data show that ringtailed lemurs preferentially orient their eyes toward other lemurs and, moreover, that they mirror the attentional state of other lemurs in their social group. Lemurs, like other prosimians, split from the main primate lineage roughly 60 million years ago and retain many ancestral primate traits (Sauther et al. 1999; Yoder and Yang 2004). Our results are thus consistent with the idea that visually-mediated social interactions have played a significant role in primate evolution and support the corollary that mechanisms of visual attention coevolved with social sophistication in primates (Jolly 1966; Allman 1999; Emery 2000). These results are also compatible with the evolution of gaze

following abilities very early in the primate lineage. When considered alongside reports of gaze following in goats (Kaminski et al. 2005), dolphins (Tschudin et al. 2001), and even ravens (Bugnyar et al. 2004), these data suggest either that gaze-following ability is widespread and evolved extraordinarily early, or that gaze-following behavior is strongly adaptive for social group-living animals and that this strong selective pressure promoted convergent evolution in these species.

It remains unclear which specific features attract lemur gaze toward other lemurs. Certainly a powerful cue toward animacy is motion. Both lemurs and humans are motile, but environmental features are not. However, it was our impres-

sion that humans and lemurs were often fixated despite staying in one place, while moving objects in the background (for example, tree branches swaying in the breeze) were not fixated. Supporting this notion, all fixations toward social targets decreased when the lemur subject was moving. We imagine this decrease reflects a change in visual priorities driven by proximate behavioral goals, but cannot exclude the possibility that low-level orienting cues (e.g., image movement on the retina) were disrupted by locomotion.

Similar uncertainty exists as to which features guided gaze following in this study. For example, while both observed head and body axes predicted gaze, only the head axis predicted gaze better after fixation than before. Two observations may explain this discrepancy. First, body axis was recorded more consistently than head axis across video clips, as demarcation of head axis was more easily disrupted by distance from the subject or small stature (usually in juvenile animals). Lemurs may be less likely to align gaze with juveniles or with lemurs that are very far away. Second, we note that the head and body axes of an animal are often, but not always, aligned—for example, in this data they tended to be well aligned when observed lemurs were moving across the scene, but poorly aligned when observed lemurs were sitting or were approaching the subjects. The discrepancy between head and body alignment suggests that when body and head cues conflict, lemurs preferentially align their gaze with the head.

These results add to the growing body of evidence (Tomasello et al. 1998; Call et al. 2003; Brauer et al. 2005; Kaminski et al. 2005; Bugnyar et al. 2004) that social attention and gaze following are not exclusive to humans. Shared attention is thought to underlie theory of mind and language acquisition, and is severely disrupted in human neurological disorders such as autism. Future gaze-tracking studies promise to bridge the gap between field observation, psychophysics, and neuroscience, and thus may play role in reconciling existing discrepancies (e.g., Klin et al. 2002; Chawarska et al. 2003; Swettenham et al. 2003; Ristic et al. 2005) between real-world and laboratory descriptions of social attention.

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http://svslab.info/reprints/shepherd&platt_S1.wmv

Video S1. Example annotated data stream. In this segment, subject Aracus looks at his female companions, moving past one to stare at a rival male neighbor. Video data were digitized at 0.22° x 33ms resolution. Clips were manually coded in a custom-designed Matlab environment (Skriatok Videoscore, svslab.info/skriatok) to extract the frame-by-frame visual coordinates of the subject's gaze (shown in **red**) and other regions of interest (ROI). Categories of ROI were selected *a priori* based on putative reward value, locomotor relevance, or social relevance: in general, markers were placed at specific positions on visible humans (**yellow**), lemurs (**blue**), food rewards (not shown here), and a small number of centrally-located, high-contrast environmental features (**green**). The end result of this coding was an annotated video sequence from which we could derive visual scanpaths, head-centered eye position, and proximity of gaze to the various categories of ROI.