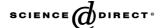


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METHODS

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Noninvasive telemetric gaze tracking in freely moving socially housed prosimian primates

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Abstract

Behavioral and neurophysiological studies strongly suggest that visual orienting reflects the integration of sensory, motor, and motivational variables. Relatively little is known, however, regarding the goals that govern visual orienting of animals in their natural environments. Field observations suggest that most nonhuman primates orient to features of their natural environments whose salience is dictated by the visual demands of foraging, locomotion, and social interaction. This hypothesis is difficult to test quantitatively, however, in part because accurate gaze-tracking technology has not been employed in field studies. We here report the implementation of a new, telemetric, infrared-video gaze-tracker to measure visual orienting in freely moving, socially housed prosimian primates (*Lemur catta*). Two male lemurs tolerated the system at approximately 1/4 body weight, permitting successful measurements of gaze behavior during spontaneous locomotion through both terrestrial and arboreal landscapes, and in both social and asocial environments. © 2005 Elsevier Inc. All rights reserved.

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1. Introduction

At the start of the last century, scientists noted that subjects do not accurately describe the eye movements they make while reading, suggesting that subjective reports cannot provide an accurate assessment of visual orienting (see [3,6]). Since then, various means of quantitatively measuring eye movements have been developed, relying initially on tracked contrast boundaries [3,6] or corneal reflections [2,13], electrooculography [3,8], currentinduction through magnetic search coils [26], and digital video oculography (see [2,20]).

In the 1960's, Alfred Yarbus dramatically demonstrated that visual orienting reflects the interaction of stimulus-driven perceptual variables with behavioral goals [35].

* Corresponding author. Fax: +1 919 668 0335. E-mail address: svs@duke.edu (S.V. Shepherd). Although his work revolutionized our understanding of the ethology of visual orienting, its scope was constrained by technical limitations. Most significantly, Yarbus tracked gaze using light reflected by mirrors, affixed by suction to the sclera of each subject, onto photo paper placed beside each picture. This technique made heroic demands on both the subjects and the experimenter, and required that subjects' heads be firmly fixed in position. Consequently, recordings were brief, focused on static two-dimensional images, and were conducted from a single vantage point with no opportunity for interaction or locomotion.

Due to its spatial accuracy and temporal precision, the magnetic search-coil technique has become widely used to study visual orienting in both humans and nonhuman primates [3]. This technique involves attaching a loop of conductive wire to the sclera so that it circumscribes the iris, the orientation of which can be measured by recording the current induced through the loop by a cycling magnetic field of known strength. The loop is surgically implanted

beneath the conjunctiva in animal experiments but is also used in humans through the application of wire-implanted contact annuli placed directly on the eye. Much as for Yarbus's optical technique, use of a magnetic search coil poses substantial design constraints that limit application to conditions outside the laboratory. First and foremost, the search-coil technique requires subjects to be held rigid within a controlled and spatially uniform magnetic field. As a result, the search-coil technique has been used to measure visual orienting only under decidedly non-naturalistic conditions (e.g., [4,11,5]). Eye movements in the laboratory are generally evoked through operant conditioning, pairing salient but artificial stimuli with explicit juice or food rewards.

Unfortunately, these limitations have resulted in a gulf between laboratory measurements of gaze behavior and the natural contexts for which gaze-control systems evolved [33,17]. For example, gaze behavior in social settings has been largely inaccessible to both laboratory scientists and field researchers (but see [14,31]; for overview see [7,12]). In the laboratory, gaze can be measured accurately, but only under conditions that typically fail to approximate the subject's natural social environment. In contrast, observations of animals in their natural social context typically rely on spatially and temporally imprecise measurements of orienting: for example, noting approximate head direction at regular intervals (e.g., [15,19,34]; for general ethological techniques, see [18]).

It has recently become possible to use portable, dual-camera, optical gaze-tracking devices to quantitatively measure the visual behavior of freely moving human subjects. This research has focused on performance of simple goal-directed tasks, for example, making sandwiches or tea [16], washing hands or filling a cup [22], copying block designs [23], and driving [30]. This research has shown that task-irrelevant fixations are rare, that fixations tend to be "just-in-time" with a buffer length of 100–1000 ms, and has reconfirmed Yarbus's [35] finding that both expectations and instructions influence the top-down constraints shaping gaze.

We aim to extend this approach to the study of visual orienting behaviors in nonhuman animals, specifically a prosimian primate, the ring-tailed lemur (Lemur catta). Ring-tailed lemurs provide excellent subjects for several reasons. First, lemurs branched from the main primate lineage in the early Eocene (50 million years ago) but are believed to retain many traits of ancestral primates and thus hint at the evolution of primate visuosocial behavior [25]. Second, lemurs are trichromats [28], have a large binocular field of 114-130° and are diurnal, despite the presence of a tapetum lucidum [25]. They live in open scrubland in societies whose complexity approaches that of anthropoid primates [28]. Specifically, they form bisexual aggregations of 10-20 individuals which are characterized by well-defined social hierarchies and extensive use of auditory, olfactory, and visual communication [28]. The importance of both olfaction and vision to social communication in this species is strikingly embodied by the large, high-contrast, musk-loaded ringtail that serves as the species' namesake. The tails are used in ritualized combat to flick scent toward the heads of rivals [25] and appear also to facilitate group cohesion—on the ground lemurs lift their tail high, while in the trees they allow their tails to hang; in both poses, the tails are conspicuous. Finally, the species is trainable, moderately sized, and tolerant of both experimenters and equipment, and subjects are readily accessible through the conservation and research programs of the Duke University Primate Center, a naturalistic but experimentally tractable setting (e.g., [21]).

2. Approach

2.1. Gaze-tracking equipment

To record gaze in freely moving nonhuman animals, we implemented a prototype optical telemetric gaze-tracker developed by Iscan, Inc. (ETL-200 Primate Research Eye Tracking Laboratory with Telemetry Upgrade). To our knowledge, this is the lightest of the few telemetric gaze-tracking systems yet developed; most competing systems are designed for human use and rely on portable recorders (e.g., the RIT Wearable Eyetracker, see [1]) rather than wireless transmitters. The Iscan system consists of headmounted eye and scene imaging systems, imported through the included RK-726PCI card into a Dell computer system for processing by raw eye-movement data acquisition software, and echoed for display to an eye and a scene monitor.

Optical gaze tracking relies on the differential reflection of invisible infrared light by the pupil and retina relative to the sclera and iris. Gaze-recording systems either track a bright pupil or dark pupil depending on their design; we used a dark-pupil system that is more resistant to changes in ambient infrared illumination than existing bright-pupil alternatives. The Iscan gaze-tracker uses two small headmounted CCD cameras: a color "scene camera" to record the $76^{\circ} \times 52^{\circ}$ view directly in front of the subject's head, and an infrared "eye camera" to record the position of the eye via a small head-mounted dichroic ("hot") mirror. An infrared LED, mounted directly beneath the eye camera, ensured adequate illumination. These components were mounted on a thermoplastic helmet specially fitted for Lemur catta (Fig. 1A). An insulated wire connected this headgear to the power supply and a radio-frequency wireless transmitter (Fig. 1B), which were worn in a backpack made from a modified primate vest (LOMIR), pouch (LOMIR), and velcro support belt.

Eye position was computed at the receiving station. First, the camera image was thresholded in software to isolate the dark pupil from the brighter iris and cornea surrounding it. Optional use of a corneal reflection (the first Purkinje image) to track eye position was abandoned, both because it is inaccurate at eccentric eye positions (Rikki Rasdan, Iscan, personal communication) and because it was easily disrupted by glare from direct sunlight. The

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