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GAZE SHIFTS AND FIXATIONS DOMINATE GAZE BEHAVIOR OF WALKING CATS

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Abstract—Vision is important for locomotion in complex environments. How it is used to guide stepping is not well understood. We used an eye search coil technique combined with an active marker-based head recording system to characterize the gaze patterns of cats walking over terrains of different complexity: (1) on a flat surface in the dark when no visual information was available, (2) on the flat surface in light when visual information was available but not required for successful walking, (3) along the highly structured but regular and familiar surface of a horizontal ladder, a task for which visual guidance of stepping was required, and (4) along a pathway cluttered with many small stones, an irregularly structured surface that was new each day. Three cats walked in a 2.5-m corridor, and 958 passages were analyzed. Gaze activity during the time when the gaze was directed at the walking surface was subdivided into four behaviors based on speed of gaze movement along the surface: gaze shift (fast movement), gaze fixation (no movement), constant gaze (movement at the body's speed), and slow gaze (the remainder). We found that gaze shifts and fixations dominated the cats' gaze behavior during all locomotor tasks, jointly occupying 62–84% of the time when the gaze was directed at the surface. As visual complexity of the surface and demand on visual guidance of stepping increased, cats spent more time looking at the surface, looked closer to them, and switched between gaze behaviors more often. During both visually guided locomotor tasks, gaze behaviors predominantly followed a repeated cycle of forward gaze shift followed by fixation. We call this behavior ''gaze stepping''. Each gaze shift took gaze to a site approximately 75–80 cm in front of the cat, which the cat reached in 0.7–1.2 s and 1.1–1.6 strides. Constant gaze occupied only 5–21% of the time cats spent looking at the walking surface.

Key words: locomotion, eye movement, head movement, constant gaze, travel fixation, motor control.

INTRODUCTION

Vision is important for successful locomotion, especially when navigating through complex natural environments. Many studies were conducted with a goal to determine how visual information is collected during locomotion, and three major types of gaze behaviors were described: fixations on objects, gaze shifts, and constant gaze. Fixations are believed to be periods when visual information is gathered about objects (e.g., Land and Hayhoe, 2001). Constant gaze occurs when during locomotion a subject looks a fixed distance ahead (Fowler and Sherk, 2003); this behavior is also called ''travel fixation'' in humans (Patla and Vickers, 1997, 2003). During constant gaze, images of objects travel across the retina in a constant pattern, and many studies suggest that such ''optic flow'' provides useful information about both the objects in the environment and the subject's own movement (Gibson, 1958; Lee, 1980). Gaze shifts, also known as gaze saccades, are rapid gaze movements between fixations and constant gaze episodes, and visual sampling has been shown to be significantly suppressed during gaze shifts (Bridgeman et al., 1975; rev. in Wurtz, 2008). While both gaze fixations and constant gaze are thought to be behaviors, during which visual information is collected, reports on how much gaze fixations and constant gaze are used during locomotion differ.

In both humans and animals, a substantial amount of data suggest that constant gaze and optic flow information play major, if not the dominant, roles in guiding locomotion (e.g., Sun et al., 1992; Sherk and Fowler, 2000; Warren et al., 2001; Srinivasan and Zhang, 2004; Mulavara et al., 2005b). This was reported to be the case not only for determining the direction or speed of locomotion, but also for gathering information about irregularities on the walking surface for accurate foot placement. For example, Sherk and Fowler (2001) showed that strobe lighting that disrupts optic flow also interferes with cats' ability to step accurately on a cluttered pathway. The same authors, inferring cats' gaze movement from movement of the head, reported that cats

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Abbreviations: CPG, central pattern generator; GLM, generalized linear model; LED, light emitting diode.

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rarely fixate on any point during walking along that cluttered pathway and spend 48–71% of time in constant gaze (Fowler and Sherk, 2003). Similarly, when studying how people use vision during stepping on irregularly placed targets, Patla and Vickers (2003) found that subjects use ~60% of their time on constant gaze, while fixating gaze on stepping targets only 14–16% of the time. It was also shown that obstacles suddenly appearing on the walking path can be successfully overstepped during locomotion even if gaze had never fixated on them (Marigold et al., 2007). These observations lead many researchers to believe that fixation of gaze on the walking pathway or on objects on this pathway is not required for accurate stepping on complex surfaces, and that both humans and animals gather most of the visual information necessary to guide stepping on such surfaces from optic flow. However, the results of other studies suggest that the ability of individuals to rely on optic flow for accurate stepping depends on the complexity of the walking surface. For example, when people were instructed to avoid stepping on cracks in the pavement, they fixated gaze on the walkway approximately two times per step (Land, 2006); and when walking on complex multi-surface pathways, which included slippery, tilted, and rocky patches, they spent less than 1% of the time in constant gaze, and made approximately three fixations of 100 ms or longer for every meter of traversed pathway (Marigold and Patla, 2007). Similarly, when people needed to step accurately on a series of irregularly placed stepping stones, they made a saccade to each stone in the sequence and fixated gaze on it before making a step (Hollands et al., 1995; Hollands and Marple-Horvat, 1996, 2001). Based on these data, it is tempting to conclude that during relatively simple tasks, constant gaze is the strategy of choice, while in comparatively difficult tasks, the constant gaze strategy is abandoned and gaze fixations and shifts prevail.

However, in addition to the above studies that focused on gaze patterns in rich visual environments, several studies have shown that both humans and animals move their gaze substantially even during the simplest locomotor task possible from a visuomotor coordination perspective, walking on a flat surface in darkness. For example, Collewijn (1977a,b) found that the gaze behavior of cats and rabbits moving around in a darkened box consisted almost entirely of shifts and fixations. Experimenting with rhesus and cynomolgus monkeys running on a circular platform and not facing any requirements for accurate foot placement, Solomon and Cohen (1992b) found that animals moved their gaze continuously, even in the darkness.

The considerable diversity in experimental tasks, data recording, and analysis techniques in previous studies and disagreement of their results is sufficient for one to still wonder what gaze behaviors take place during normal unobstructed locomotion when there is no specific visual task and how these behaviors are modified with the introduction of objects and stepping targets. Accurate recording of gaze in unrestrained subjects has consistently proven to be a challenge, but advancements in *wearable* scleral search coil-based eye-tracking technology has made high frequency and precision recordings of eye movements in freely walking subjects possible (Ogorodnikov et al., 2006). A miniature head-mounted magnetic field generator and eye coil signal decoder for recording the rotation of the eye in the orbit, coupled with a three-dimensional head movement-tracking technology have allowed us to record both eye and head movement during overground locomotion in the unrestrained cat at high temporal resolution (200 Hz) and to calculate gaze direction and gaze/ground intercept locations with high accuracy. Using this new technology we have re-examined the gaze strategy during walking. We hypothesized that cats will exhibit distinct gaze behaviors in environments where the visual complexity of the walking surface and the accuracy requirements for foot placement differ. We have studied cats because they are the closest animals to humans whose unconstrained locomotion behavior can be fully researched in the laboratory, and because they are classic subjects for studies of both visual and motor systems.

In this report, we first describe the gaze behaviors of cats walking on a flat surface in complete darkness, where visual information was neither needed nor available to guide walking. We then describe the gaze behaviors employed during locomotion over the same surface in light, where visual information was available but not necessary to guide stepping. Next, we present data on the cat gaze behavior during walking along the highly but regularly structured and familiar surface of a horizontal ladder, a task for which we have previously shown that step-by-step visual guidance is required. Finally, we demonstrate how cats use their gaze when traversing a walkway cluttered with many small stones placed in a new haphazard pattern every trial, a complex but natural everyday task for land-living creatures. Our main finding is that, in all these environments, cats predominantly use gaze shifts and fixations, not constant gaze, to aid their walking, and that, as the visual complexity of the environment and the demand on visual guidance of stepping increase, cats spend more time looking at the surface, look closer to themselves, and shift between gaze behaviors more frequently.

A brief account of this study was published in abstract form (Rivers et al., 2009).

EXPERIMENTAL PROCEDURES

Recordings were obtained from three adult cats (two females: cat 1 (3.7 kg) and cat 3 (3.0 kg) and a male, cat 2 (4.0 kg)). All experiments were conducted in accordance with NIH guidelines and with the approval of the Barrow Neurological Institute Animal Care and Use Committee.

Locomotion tasks

Positive reinforcement via food was used to adapt cats to the experimental situation and engage them in locomotor behavior (Skinner, 1938; Pryor, 1975). Cats walked in a 2.5-m-long-by-0.6-m-wide chamber (Fig. 1A–C). A longitudinal wall divided the chamber into two corridors that