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Rhesus Monkeys Behave As If They Perceive the Duncker Illusion

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Abstract

The visual system uses the pattern of motion on the retina to analyze the motion of objects in the world, and the motion of the observer him/herself. Distinguishing between retinal motion evoked by movement of the retina in space and retinal motion evoked by movement of objects in the environment is computationally difficult, and the human visual system frequently misinterprets the meaning of retinal motion. In this study, we demonstrate that the visual system of the Rhesus monkey also misinterprets retinal motion. We show that monkeys erroneously report the trajectories of pursuit targets or their own pursuit eye movements during an epoch of smooth pursuit across an orthogonally moving background. Furthermore, when they make saccades to the spatial location of stimuli that flashed early in an epoch of smooth pursuit or fixation, they make large errors that appear to take into account the erroneous smooth eye movement that they report in the first experiment, and not the eye movement that they actually make.

INTRODUCTION

The visual system uses retinal motion to analyze the motion of objects in the world, and the motion of the observer him/herself (Gibson, 1966). When an object moves across a stationary background, the human visual system perceives that object to be moving and the background to be stationary. When the visual background moves across the retina in certain stereotypical ways, the human visual system perceives that the observer is moving.

Karl Duncker (1929) showed that when a stationary object on the retina is embedded in retinal background motion, the subject perceives the object to be moving in a direction opposite from that of the background. Anyone can see this on a partially cloudy night, when the clouds streaming by the moon cause it to appear to be moving in the direction opposite that of the clouds.

A more complex variant of the Duncker Illusion occurs when both the object and the background move. In that situation, the background adds an illusory component in the direction opposite that of the background motion, which sums with the true motion. For example, if the object moves horizontally and the background moves upward vertically, then the object will be perceived to have an illusory downward vertical component resulting in a perceived diagonal trajectory (Zivotofsky, Averbuch-Heller, et al., 1995).

The Duncker Illusion is a useful research tool because it neatly separates veridical from perceived motion. Various studies have investigated its effect on the human ocular motor and arm movement systems. This extremely robust illusion has been quantified by means of the “slant matching method” (Post, Chi, Heckmann, & Chaderjian, 1989; Post, & Chaderjian, 1988), and by cancellation of the illusion (Zivotofsky, 2004). When normal humans track the moving object using smooth pursuit, they report that their eyes follow the diagonal motion of the target, although measurement of their eye movements reveals that their eyes in fact follow the target veridically. In combined eye–head tracking, the head is influenced by the illusion with the head following the perceived motion while the eyes remain on the pursued target (Zivotofsky, Averbuch-Heller, et al., 1995). In a saccade-to-remembered-target task, humans exhibit large errors if the target is flashed during an epoch of the illusion, behaving as if they are generating the saccade from the illusory rather than true eye position (Zivotofsky, White, Das, & Leigh, 1998; Zivotofsky, Rottach, et al., 1996). The illusion causes hand-pointing errors as well (Soechting, Engel, & Flanders, 2001).

In this study, we asked whether Rhesus monkeys, whose oculomotor and visual systems are often used as a model for those of the human (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman, 1992), also behave as if they perceive the Duncker Illusion. We trained monkeys to report the direction of their own smooth pursuit, and to make saccades to targets that flashed briefly early in an epoch of pursuit across an orthogonally moving background. We found that, indeed, monkeys report the effects of the Duncker Illusion despite pursuing the targets accurately, and that their memory-guided saccades compensate for the trajectory that they report rather than the trajectory that they actually make.

Brief reports of these experiments have been reported elsewhere (Powell, Zivotofsky, & Goldberg, 1999; Zivotofsky, Powell, & Goldberg, 1998).

RESULTS

Experiment 1: Does a moving background affect the monkeys’ report of the direction of motion of a pursuit target?

We trained the monkeys to pursue a target moving vertically, or slightly deviated from the vertical. At the end of the pursuit epoch, the monkeys had to make a saccade to the right or left depending on the direction from which their pursuit trajectory deviated from the vertical. After extensive training, the monkeys were able to achieve accuracies of over 70% with offset angles as small as 5°. When the offset angle was greater than 10° the monkeys performed almost perfectly. When the target moved perfectly vertically the monkeys made random choices. During experimental sessions the offset angle varied from –15° (leftward deviation) to 15° (rightward deviation).

After the monkeys had learned to report their pursuit direction in this nonillusory task, they had to make the same type of discrimination when the pursuit target moved across a stationary or horizontally moving random-dot background (Figure 1). There were two parts to this experiment. In the first, the background was either stationary or moved rightward or leftward at 5°/sec while the target moved upward, either purely vertically or nearly so.

The background motion affected the monkeys’ report of their own pursuit direction. A typical example for the three background conditions is shown in Figure 2. When the background was stationary, the monkeys performed accurately. When the background moved rightward, its motion contributed a leftward component to the reported horizontal offset of vertical target motion. Therefore, for small rightward angles for which the monkey would have previously responded correctly, the monkey now more frequently reported leftward movement of the target. Similarly, when the background moved leftward, background motion contributed a

rightward component that led the monkey to report rightward target motion for trials in which the target actually had a small leftward angle.

When the target moved purely vertically with no horizontal offset, the monkeys' reports were affected by the second variable—velocity of the background motion (Figure 3). In this experiment, the target always moved purely vertically and the background had a variable velocity, from 20°/sec (rightward), to −20°/sec (leftward). Some trials had a stationary background. When the background was stationary, the monkeys made random guesses. When the background had a rightward movement (positive velocity in the figure), the monkey reported leftward target and pursuit movement, and the faster the movement, the stronger the reported leftward component. When the background moved leftward, it contributed a rightward component that increased with speed.

Experiment 2: Does a moving background affect the accuracy of saccades to remembered targets?

Monkeys make reasonably accurate saccades to targets that flash briefly before an intervening epoch of smooth pursuit (Schlag, Schlag-Rey, & Dassonville, 1990), suggesting that they have a veridical representation of their own pursuit trajectory. We trained the monkeys to make saccades to remembered targets that were flashed either during fixation or early in an epoch of 10°/sec horizontal smooth pursuit. The fixation/smooth pursuit target began each trial centered vertically on the screen and either centered horizontally or 10° on either side of the horizontal center. Initially, the monkeys had to make these saccades to remembered targets in the absence of a random-dot background (Powell, Zivotofsky, & Goldberg, 1998). We then studied the effect of a moving background on the accuracy of memory-guided saccades. On some trials, the background began to move 8°/sec vertically at the same time that the pursuit target started moving horizontally across the screen. After 1000–2000 msec the pursuit target and background disappeared, and the monkey had to make a saccade to the remembered location of the flashed stimulus (Figure 4). During training sessions, with either no background or a stationary background, the monkey had to land within a window of 10° to receive a reward. On the experimental trials, we enlarged the window to 20° in the vertical dimension, the direction in which we anticipated errors, to permit the possibility of systematic saccadic error, while the horizontal dimension remained 10°. The monkey received no other feedback about the accuracy of its saccade during the experimental trials.

In contrast to Experiment 1, which had a pursuit target moving upwards across a horizontally moving background, in these experiments we used a pursuit target moving horizontally across a vertically moving background.

We found that the direction of background motion did affect the accuracy of the saccadic eye movements. When the background moved downwards, a situation in which the monkey would have, as shown in the previous experiment, reported an upward component to eye and target trajectory, the subsequent saccade to the remembered target landed below the target. When the background moved up, resulting in a perceived downward eye and target trajectory, the saccades landed above the target. In both of these cases, the monkey behaved as if the oculomotor system compensated for a perceived eye movement that the monkey did not actually make (cartoon in Figure 5).

Figure 6 plots the beginning and end of saccades to remembered targets after an epoch of pursuit. In this example, the monkey pursued from left to right, and the beginning points of the saccades are clustered together at the right side of the figure. Saccades made to the remembered target location are not completely accurate even when the background did not move. As previously shown, the vertical error of saccades to remembered targets is proportional to the duration of the delay period (Stanford & Sparks, 1994; Gnadt, Bracewell, & Andersen, 1991).

The filled circles are the saccades to a target 5° above vertical, in the absence of background motion. They have a mean vertical component of $6.33^\circ \pm 0.94^\circ$.

During background motion there is a very small, albeit significant, effect of background motion on pursuit trajectory, with an offset in the direction of the background motion: Upward motion was associated with a slight upward deviation of the eyes, and downward motion with a slight downward deviation of the eyes. There is a much greater effect of the background motion on the endpoint of the saccades: Upward background motion was associated with a mean vertical component of $9.44^\circ \pm 1.70^\circ$ and downward motion with a mean vertical component of $3.70^\circ \pm 3.09^\circ$. In all three conditions (background up, background down, and stationary background), the remembered target was flashed at 5° vertical. Figure 7 shows average saccadic landing position for two series of trials.

DISCUSSION

The results of these experiments strongly support the contention that Rhesus monkeys perceive the Duncker Illusion and that their saccadic system is influenced by it.

In Experiment 1, the monkeys were asked to report the side to which an almost-vertical pursuit target trajectory deviated from the vertical. This judgment was distorted in the same way the Duncker Illusion distorts judgment in humans: The subjects report that the target has a component of motion opposite the background motion (Zivotofsky, 2004). In the monkeys this error in judgment was manifest as a distortion in their report of the trajectory of the vertically moving target, and it became more intense as background speed increased. Despite the monkey's report, its actual pursuit was quite accurate. The results of this experiment do not enable us to distinguish whether the monkeys were reporting the trajectory of the stimulus or of their own (perceived) eye movement. Humans perceive that their eye movements are distorted (unreported observation of the authors and of their colleagues) by background motion as well as their perception of target motion as originally described by Duncker (1929).

We used Experiment 2 to establish that the monkeys had an erroneous internal representation of their own eye movements. In this experiment, we showed that when monkeys made saccades to remembered targets that were flashed either during an epoch of pursuit across a moving background or during fixation while the background was moving, their saccades were grossly inaccurate. They would land above the target when the background moved down and below the target when the background moved up. When monkeys pursued a spot moving orthogonal to a moving background, their pursuit was slightly affected by the background, such that there was a mean displacement in the direction of background motion. This was presumably because of an optokinetic effect. However, this effect was minimal compared to the distortion in the amplitude of remembered saccades. In addition, it was in the wrong direction: Downward background motion is associated with a slight downward optokinetic effect, but with a perceived upward movement of the target. Thus, the saccadic error could not have occurred as a result of an optokinetic drag. Instead, we suggest that the error arises from a misjudgment of the monkey's eye trajectory evoked by the Duncker Illusion, similar to the monkey's erroneous report of their own pursuit trajectory under similar conditions. The monkeys then program the saccade from the illusory final eye position rather than the true position (as in Figure 5). The monkeys' range of saccadic errors was within the range of saccadic errors made by humans in a similar experiment (Zivotofsky, White, et al., 1998; Zivotofsky, Rottach, et al., 1996; White, Sparks, & Stanford, 1994).

The nervous system, and in particular the visual system, of various animals, and in particular nonhuman primates, is often used as a model for the human system, one in which more invasive experiments can be performed. It is thus of great importance to know how the animal perceives

a particular stimulus. There have been many reports of animals that report a variety of visual illusions. Baboons report the Corridor Illusion: When there is a perceptual dissonance between size and distance, they assume that distance is veridical and adjust perceived size (Barbet & Fagot, 2002). The report of illusory contours has been found in monkeys, cats, owls, and bees, and in all of them a neural correlate has been described (Nieder, 2002). The Ponzo Illusion, in which the upper of two equal lines appears longer when placed between inverted “V” context lines, has been shown to be perceived by pigeons (Fujita, Blough, & Blough, 1991), monkeys (Bayne and Davis, 1983), and horses (Timney & Keil, 1996). However, when Fujita (1997) compared the strength of various permutations of this illusion in rhesus monkeys, chimpanzees, and humans, he was able to demonstrate that although both monkeys and chimpanzees report the illusion, the strength of the illusion did not vary as predicted based on the classic understanding of its mechanism. Neither monkeys nor chimpanzees responded as expected. Nonhuman primates report the Ponzo Illusion, but not in the same manner as humans. Auditory illusions, such as amodal completion of biologically meaningful acoustic stimuli, have been demonstrated in the tamarin monkey (Miller, Dibble, & Hauser, 2001).

In this study, we have added an additional visual illusion that is reported by monkeys and available for further study. The Duncker Illusion and the response to it are important for several reasons. They show that given a dissonance between an internal estimate of eye movement and a compelling visual illusion, monkeys, like humans, allow the erroneous visual perception to override a veridical corollary discharge. This illusion neatly separates perceived target trajectory from true motion and offers an opportunity to study the updating of spatial maps. It demonstrates that the visual system seems to rely on an assumption of a background that is a stable, reliable frame of reference, and that this assumption can lead to illusory motion of a foreground target, thus affording the chance to examine target/background selection strategies.

The physiology of spatial vision in the Rhesus monkey is relatively well understood (Colby & Goldberg, 1999). Our demonstration that monkeys show the effects of the Duncker Illusion, both in their report of target trajectory across a moving background, and in the saccadic error evoked by a moving background, in ways qualitatively similar to humans, clears the way for a better understanding of this illusion at the physiological as well as at the psychological level. Do monkeys perceive the Duncker Illusion? Caution should force us to avoid such an anthropomorphic conclusion; yet if the monkey brain has any relevance to the human we must ultimately argue that a shared behavioral report represents shared perception.

METHODS

A total of three male Rhesus monkeys (*Macacca mulatta*) were used in this study. Each monkey was trained to sit quietly in a primate chair and to fixate stationary targets, to follow moving visual stimuli, or to make saccades to remembered target locations for fluid reward (Wurtz, 1969). The visual stimulus was the image of a rear-projected LED or laser 0.3° in diameter with a mean luminance of 2 cd/m² controlled by a General Scanning servo-controlled mirror galvanometer driven by a D/A converter with an update rate of 1 kHz (as in Powell & Goldberg, 2000). When present, the background was a random pattern of white dots that either moved horizontally with 100% coherence, or remained stationary. The dots were rear-projected on a screen by an NEC DLP projector with a pixel density of 800 × 600 using graphics software developed in open GL, running on a Silicon Graphics PC-based computer.

The animals were prepared for eye position recording during sterile surgery under ketamine-induced, isoflurane anesthesia. Each animal was implanted with a plastic recording chamber, a head holder for restraint of the head during recording, and eye coils that allowed the measurement of eye position (Judge, Richmond, & Chu, 1980). They were allowed to recover completely before training and experiments were conducted. All protocols were approved by

the Animal Care and Use Committee of the National Eye Institute and were in compliance with the Public Health Service Guide for the Care and Use of Laboratory Animals.

Behavioral control, data recording, and preliminary data analysis were performed on a personal computer using the REX system (Hays, Richmond, & Optican, 1982), and further data analysis was performed off-line using Matlab.

Two series of experiments were performed in which a moving target was given an illusory component due to a moving background. For technical reasons, in Experiment 1 there were horizontal illusory deflections of a vertically moving dot and in Experiment 2 there were vertical illusory deflections of a horizontally moving dot.

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Figure 1.

Task in Experiment 1. The monkey was required to fixate the fixation point (FP) and then to track it as it moved slowly either vertically or nearly vertically with a small horizontal offset. The random-dot background either remained stationary or moved rightward or leftward. At the conclusion of the pursuit, both the FP and background were extinguished and two targets appeared, one to the right and one to the left of the center. The monkey was required to execute a saccade to the target on the side to which the pursuit target veered.

Figure 2.

The monkey's report of the direction of the horizontal component of the vertically ascending target. Note that when the background moved rightward (down-pointing triangles) it induced a leftward component in the target motion, resulting in fewer reports of motion to the right. Thus, even when the target was moving up with a small rightward angle the monkey was likely to report it as having a leftward component. Similarly, leftward background motion added a significant rightward component.

Figure 3. Results of varying the background velocity when the target moved purely vertically. Note that the greater the rightward velocity the greater the propensity for the monkey to see the target with a leftward trajectory.

Figure 4.

Experimental paradigm for Experiment 2. The trials began with a monkey fixating the fixation point (FP). It then either remained stationary or began to move horizontally. In either case, the monkey was required to remain on the target, either with fixation or by following it with smooth pursuit. During this period the background of random dots was either stationary or moved vertically. Early in this period a target flashed in the monkey's visual periphery. The monkey was required to ignore the flashed target and continue looking at the FP. At the conclusion of this period the FP and background were extinguished and the monkey was required to saccade to the remembered location of the flashed target.

Figure 5.

Graphic showing the proposed explanation for the erroneous saccades. The oculomotor system involved in generating saccade prepares a saccade of the size and direction required based on the perceived pursuit, despite the fact that such pursuit did not actually occur. That planned saccade is then executed from the termination point of the actual pursuit, resulting in the gross error observed.

Figure 6.

An x - y plot of the eye positions at the start of the saccade (end of pursuit) and at the end of the saccade. Note that when the background moved up there was overshoot, when the background moved down there was an undershoot, and the landing position when the background was stationary was between those two populations.

Figure 7. x - y plots of the average (and SD) eye position at the start of the saccade (end of pursuit) and at the end of the saccade for rightward (A) and leftward (B) pursuit.