INTRODUCTION

There are two common situations during which we employ visual tracking to avoid excessive retinal image motion (Kawano 1999). One is to compensate for self-movement, and the other is to follow the object of regard when it moves. In the latter case, subjects can successfully track a target that moves across a stationary textured background, even though this generates contrary motion of the background images on the retina (reafference) that competes with the motion of the target’s retinal image, potentially disrupting the tracking of the target. Previous work on humans reported that brief perturbations of the background in the opposite direction to pursuit were much less disruptive than perturbations in the same direction as pursuit. Furthermore, if the background moved together with the pursuit target—so as to effectively eliminate the reafference—then the effects of a subsequent background perturbation showed less dependence on direction. This suggested that the direction selectivity to background perturbations during pursuit against a stationary background was due, at least in part, to the prior motion of the background secondary to the pursuit. We now report similar findings in monkeys, and in addition, have investigated the effect of moving the background while the animal was fixating a stationary target. In this situation, the ocular tracking responses to subsequent brief perturbations of the moving background were weaker when the perturbations were in the same direction as the prior background motion than when in the opposite direction. This suggests that the selective insensitivity to the reafferent visual input associated with pursuit across a stationary background is, at least in part, independent of pursuit per se and attributable to a progressive reduction in the sensitivity to sustained background motion.

METHODS

Data were collected from four adolescent Japanese monkeys (Macaca fuscata), weighing 4–8.5 kg. All procedures reported here were approved by the Institute’s Animal Care and Use Committee. Many of the general procedures were the same as those used in previous studies by Schwartz and Lisberger 1994 on monkeys and Churchland and Lisberger 2002 on humans, who showed that the pursuit responses to perturbations of the target were greater if the target was moving and being tracked by the subject than if it was stationary and being fixated by the subject. These observations led to the suggestion that there are at least two mechanisms that can influence the gain of tracking. One that increases the responses to target motion nonspecifically whenever the pursuit system is actively engaged, independent of the background. Another is that influences tracking performance by selectively reducing the tracking system’s sensitivity to the visual reafference are associated with pursuit across a stationary background.

This study shows that the responses of monkeys to background perturbations are qualitatively similar to those of humans, indicating that they would provide a good animal model for humans. Monkeys are selectively less sensitive to background motion that induces retinal slip in the same direction as the reafferent visual motion normally associated with pursuit across a stationary textured background and also show a relatively nonselective increase in sensitivity to motion during pursuit when the background moves with the target. We also report that, when the animal fixates a stationary target, sustained background motion selectively reduces/increases the sensitivity to subsequent background perturbations in the same/opposite direction.

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
of ocular tracking in monkeys and humans (Kawano et al. 1992; Miles et al. 1986; Suehiro et al. 1999) and so will only briefly be given. The monkeys were previously trained to fixate a small spot. Under pentobarbital sodium anesthesia and aseptic conditions, each monkey was implanted with a head holder, which allowed the head to be fixed in the standard stereotaxic position during the experiments, and with scleral search coils for measuring eye movements (Judge et al. 1980). Animals faced a translucent tangent screen, which was 52 cm in front of the eyes, and the area visible to the animal was limited by the edges of the frame of the eye coil system, which subtended 85° along the vertical and horizontal meridia. Two red LED spots were back-projected onto the screen by two independent projectors, one to act as a target for fixation and the other for pursuit. The target spots subtended 0.5° of visual angle. A random dot (background) pattern was also back-projected onto the screen by a slide projector, filling the screen except for a horizontal band (1° wide) centered on the fixation target to facilitate the pursuit of the (horizontally) moving target. The dots in the background subtended ∼0.8° of arc, and the luminance ranged from 6.5 (white dots) to 0.6 cd/m² (black surround areas). The horizontal and vertical positions of the pursuit target and the background were independently controlled by mirror galvanometers in the projector light paths. In one experiment, the random-dot background images were partitioned into central and peripheral parts, each controlled independently by a separate slide projector with its own mirror galvanometer (center, 15° diam).

Data collection and analysis

The presentation of the stimuli and the collection, storage, and display of data were controlled by a PC running the REX operating system (Hays et al. 1982). Eye movements were measured using the electromagnetic search coil technique (Fuchs and Robinson 1966). Voltage signals encoding the horizontal and vertical components of the eye position, together with mirror (galvanometer) position, were passed through an analog filter (200 Hz) and were digitized to a resolution of 12 bits and sampling at 1 kHz. All data were stored and transferred to another PC for analysis using an interactive computer program based on Matlab (Mathworks). Eye position data were differentiated to yield eye velocity profiles (differentiator 80 Hz, −3dB). Trials free of saccades for the first 500 ms following the onset of target motion were selected for further analysis. To obtain low-noise estimates of eye velocity, responses were averaged over ≥20 trials free of saccades. The mean eye velocity profiles were differentiated using a digital filter to yield eye acceleration profiles (differentiator 80 Hz, −3dB). The mean eye velocity profiles (after subtracting the no-perturbation controls) were used to estimate the mean initial peak eye velocity, which was the maximum eye velocity achieved by the first wave of eye acceleration (Miles et al. 1986). The initial peak eye velocity was searched in the 100-ms interval starting 60 ms after the onset of the perturbation. Note that the latency of the responses was ∼60–70 ms (e.g., Fig. 1). The trial-by-trial variance was computed by measuring the eye velocity at the time of the initial peak in the mean eye velocity profile.

Behavioral paradigms

We recorded the ocular tracking elicited by brief background motions (perturbations) and investigated their dependence on the prior visuo-motor conditions in three separate paradigms. At the start of each trial, a stationary fixation target appeared at the center of the screen along with a stationary random-dot pattern that provided a textured background. The animal was required to position its eyes within 2° of the fixation target for a variable period of time for the trial to proceed. The subsequent events varied from one paradigm to another and were as follows.

OCULAR TRACKING RESPONSES TO BRIEF PERTURBATIONS OF A PREVIOUSLY STATIONARY TEXTURED BACKGROUND WHILE ATTEMPTING TO PURSUE A MOVING TARGET. The central fixation target disappeared and another identical target appeared at an eccentric position (1–5°, right or left of center) moving toward or away from the screen center at one of several possible fixed speeds, which was called the step-ramp paradigm (paradigm 1) (Lisberger and Westbrook 1985; Rashbass 1961). The monkey was required to track the moving target and to keep its eyes within 2° of the target’s location. Our interest here was solely in the case in which the target moved toward the screen center because it often resulted in the initiation of smooth tracking free of catch-up saccades, but on 50% of trials, the motion of the target was away from the fovea to ensure that the direction of motion could not be predicted from the direction of the step. The step size (1–5°), that is, the initial eccentric position of the pursuit target, was selected separately for each animal and for each speed and direction of pursuit to minimize the likelihood of catch-up

FIG. 1. Ocular responses to a sudden movement of the background. A: background moved rightward at 60°/s for 40 ms when monkey 55 pursued a target moving at 20°/s in the right direction. Background started moving 300 ms after the onset of target motion. Traces are superimposed horizontal eye velocity profiles (n = 21) and average horizontal eye velocity profile (thick line). Bottom traces: velocity profiles of the target (thin line) and background (thick line) motion. B: average eye velocity profile in A (thick line) is plotted with control (thin line; pursuing a target moving at 20°/s in the right direction without the perturbation) to clarify the eye velocity responses to the perturbation. Bottom traces: velocity profiles of the target (thin line) and background (thick line) motion.
saccades. The speed of the target (ramp) was 0, 5, 10, 20, or 30°/s. (Note that, to avoid a saccade in the special case of 0°/s, the target at the center stayed on and was not replaced by one at an eccentric position.) Two hundred fifty milliseconds (or 300 ms for 1 monkey) after the onset of target motion, the background was perturbed horizontally, moving at one of several possible fixed velocities for 40 ms. After the target had been moving for 800 ms, the target and the background were turned off, indicating the end of the trial, and the animal was given a drop of fruit juice. In an additional variant of this paradigm, we arranged for the speed of the background perturbations to always differ from the speed of the target by 60°/s (rightward or leftward), regardless of the preceding target/background velocity. All experiments included control trials in which the perturbation of the background was omitted.

**Ocular tracking responses to brief perturbations (speed changes) of a textured background while attempting to pursue a target that was moving together with that background.** As in the first paradigm, the central fixation target disappeared and another identical target appeared at an eccentric position (1°–5°, right or left of center) moving toward or away from the screen center. In the present paradigm (paradigm 2), however, the background also started to move at the same time as the target and with the same speed and direction (0, 5, 10, or 20°/s, rightward or leftward). Two hundred fifty milliseconds after the onset of motion, a brief perturbation of the background was applied by adding a rightward or leftward movement of 60°/s to the pre-existing background motion for 40 ms. The motion of the target was not changed. After the target had been moving for 800 ms, the target and the background disappeared, and the animal was given a drop of fruit juice, indicating the end of the trial. In one further experiment, the random-dot pattern on the screen was partitioned into a circular central region 15° across and a surrounding peripheral region, each produced by a separate slide projector and controlled independently by mirror galvanometers in the light paths. This permitted us to restrict the perturbations to the central or peripheral regions of the retina. All experiments included control trials in which the perturbation of the background was omitted.

**Ocular tracking responses to brief perturbations (speed changes) of a moving textured background during attempted fixation of a stationary target.** The background started moving horizontally at 20°/s, rightward or leftward, and 250 ms later, the background was perturbed briefly—its speed changing to 40°/s, rightward or leftward, for 40 ms (paradigm 3). The target and background were turned off 510 ms later, signaling the end of the trial. Control trials were included in which the perturbation of the background was omitted. The animal was required to keep its eyes within 2° of the stationary target throughout the trial, despite the background motions, and to refrain from making any saccades to receive a fruit-juice reward.

**RESULTS**

**Ocular tracking of a target moving against a stationary textured background: effects of brief perturbations of the background (paradigm 1)**

Monkeys were able to pursue targets moving against a stationary textured background, usually taking about 200 ms to reach their asymptotic tracking velocity, which in some cases was very close to the actual target velocity. Nonetheless, even when seemingly little affected by the background, their tracking could be markedly affected by subsequent brief disturbances of that background. This can be seen in the sample eye velocity tracking responses shown in Fig. 1A, in which the animal generally achieved a pursuit velocity very close to target velocity (20°/s rightward) and yet responded quite vigorously to a subsequent brief rightward perturbation of the background (duration, 40 ms; speed, 60°/s; onset time, 300 ms after the onset of the original target motion). The component of the response attributable to the perturbation is made clear in Fig. 1B, which shows the mean eye velocity tracking responses with (thick line) and without the perturbation (thin line). The responses to the perturbations of the background had the ultrashort latency characteristic of the ocular following responses elicited by background motion when the animal is not tracking a moving target (Miles et al. 1986).

**FIG. 2.** Effect of changes in background perturbation velocity on response profiles sampled from monkey 55. A: sample average eye velocity profiles resulting from application of background perturbations (40 ms, rightward) of various speeds (10, 20, 30, 40, 60°/s) during pursuit of a moving target (20°/s, rightward) against the stationary background. B: response profiles obtained by subtracting mean pursuit response to the same 20°/s target motion when no perturbation was applied from the eye velocity profiles in A. Bottom trace: velocity profile of background motion. Note that traces are aligned at the onset of background perturbations. Initial peak velocities were 1.1, 1.4, 4.8, 7.4, and 11.4°/s when the perturbation velocities were 10, 20, 30, 40, and 60°/s, respectively.

Dependence on the retinal velocity of the background during the perturbation

We examined the dependence of the responses to background perturbations on the velocity of the perturbation and show sample mean eye velocity traces for one animal—the same one illustrated in Fig. 1—in Fig. 2A. In the experiments...
that generated these sample data, all motions were rightward, the speed of the target being 20°/s in all cases and the speed of the background perturbations ranging in steps from 10 to 60°/s (see the key in Fig. 2A). The eye velocity profiles show clear dependence on the velocity of the perturbation, and to further clarify this dependence, we also show the mean eye velocity profiles after subtracting the mean response to the same 20°/s target motion when no perturbation was applied (Fig. 2B). It is now apparent that the disturbance in tracking was greatest with the highest perturbation speed that we used—60°/s—and was minimal for perturbation speeds equal to or less than the target speed of 20°/s. To quantify these effects, we measured the mean initial peak eye velocity (after subtracting the no-perturbation controls and computing the trial-by-trial variance from the raw eye velocity recorded at the time of that peak), and those data are plotted in Fig. 3A: the data seen in Fig. 2 are here shown as circle symbols. We now see that perturbations of 20°/s or less elicited only very small responses with little or no dependence on perturbation velocity. In contrast, when the perturbations were faster than the target velocity, they caused disturbances in target tracking that increased progressively with increases in the perturbation velocity. That the transition occurred when the perturbation velocity equaled the target velocity became very clear when we examined the data obtained with other target velocities. Thus when target velocities were 10 and 30°/s (rightward), responses to (rightward) background perturbations showed clear dependence on velocity only when the background speed exceeded 10 and 30°/s, respectively (Fig. 3A, squares and triangles). Clearly, the important parameter during the perturbations was the relative velocity between the target and background: if the velocities of the target and background during the perturbations were such that the target overtook the background—as during normal everyday tracking—the responses to those perturbations were almost negligibly small. Only when the velocities of the target and the background during the perturbations were such that the target was overtaken by the background—surely rare in everyday life—were there appreciable responses to the perturbations. A similar pattern of behavior was found with leftward tracking (data not shown), but of course, the signs were all reversed.

The data that we have presented so far were all obtained from a monkey whose tracking velocity at the time the perturbations were applied was always very close to the target velocity, so that the transition point in the dependence on background velocity—below which responses to perturbations were negligible and above which responses showed clear dependence on velocity—corresponded to the reversal point for the retinal image motion. (Note that the perturbations in this experiment always involved motion on the screen that was in the same direction as the target motion. Also, slow perturbations often generated weak responses in the positive direction even though the retinal slip was negative. These seemingly anomalous responses generally showed little dependence on retinal slip velocity and their etiology is unclear. One possibility is that they represent a weak response to the perturbation.

**FIG. 3.** Ocular responses to background perturbations. **A and B:** responses sampled from monkey 55. Background perturbation was applied at 300 ms after the onset of target motion. Initial peak eye velocities are plotted against background perturbation velocity (**A** and retinal slip velocity of the perturbation (**B**). Note that data from **A** are re-ploted in **B**. C–E: average data from 3 other monkeys (**C**: 57, **D**: 58, **E**: 59) plotted in the same manner as **B**. Note that the background perturbation was applied at 250 ms after the onset of target motion for these monkeys.

*J Neurophysiol* • VOL 91 • JUNE 2004 • www.jn.org
acceleration.) This suggests that, during ocular tracking, perturbations of the background affected that tracking to the extent that they induced background motion on the retina that was in the reverse direction of the normal reafference when subjects tracked a target moving against a stationary background; perturbations that induced background motion on the retina that was in the same direction as the normal reafference during pursuit were largely ineffective. To examine this, we re-plotted the data shown in Fig. 3A in terms of the retinal slip velocity, computing the latter by subtracting the mean eye velocity (during the perturbation) from the perturbation velocity (Fig. 3B). It is now clear that, when perturbations were too weak to reverse retinal slip (i.e., the rightward perturbation was slower than the rightward ocular tracking so that the retinal slip was negative in Fig. 3B), they were ineffective, and when perturbations were strong enough to reverse retinal slip (i.e., the rightward perturbation was faster than the rightward ocular tracking so that retinal slip was positive in Fig. 3B), they now had an impact, and this increased in magnitude with slip velocity. A similar dependence on retinal slip velocity was seen in three more monkeys (Fig. 3, C–E).

Dependence on the pursuit velocity

Further perusal of Fig. 3, C–E, indicates that the responses to those perturbations of the background that reversed the normal direction of the reafference on the retina during pursuit were also dependent on the target velocity at the time the perturbations were applied: the data clearly imply that, for perturbations that resulted in a given (reversed) retinal slip velocity, the greater the target velocity, the greater the response to that perturbation.

In an attempt to characterize this dependence on target velocity more clearly, especially when the target and background were moving in opposite directions, we did one additional experiment in which the speed of the background perturbations always differed from the speed of the target by 60°/s (rightward or leftward). For example, when the target moved leftward at 20°/s, the subsequent background perturbations were either 80°/s leftward or 40°/s rightward. Sample mean eye velocity response profiles to rightward perturbations are shown for one monkey in Fig. 4A. The profiles with perturbations are shown in black lines or a thick gray line for that during fixation, and the profiles without perturbations are shown in thin gray lines. Given that all of the perturbations were rightward, as reported above, the responses to those perturbations were invariably small when they induced retinal motion of the background that was in the usual direction for pursuit reafference (i.e., when the monkey fixated a stationary target or tracked a leftward-moving target) and increased in magnitude when they induced motion in the reversed direction of the usual pursuit reafference (i.e., when the monkey tracked a rightward-moving target). The tracking performance of this monkey during the times the brief perturbations were applied was generally very good, so that the retinal slip velocity during the perturbations was invariably within 2% of the applied 60°/s. Figure 4B shows these same response profiles after subtracting the mean eye velocity profiles recorded when the monkey tracked the corresponding target motions but no perturbations were applied. The initial peak eye velocity response elicited by the rightward perturbations, expressed as a percentage of the peak response to the same perturbation during fixation of the stationary target (termed percentage modulation), is plotted against target velocity in Fig. 4C (closed circles, continuous line) and shows a clear discontinuity around zero target velocity: leftward tracking—for which the retinal motion of the background during the perturbations was always in the same direction as that during pursuit across a stationary background—was almost without effect, but rightward tracking—for which the retinal motion of the background during the perturbations was in the opposite direction to that during pursuit across a stationary background—increased the responses to the perturbation, and the greater the tracking velocity the greater its impact. Similar findings, with the opposite sign, were obtained with leftward perturbations (Fig. 4C, open circles and discontinuous line). Thus the enhancement of the responses to background perturbations during pursuit were also dependent on the target/pursuit velocity, prior tracking selectively increasing the sensitivity to background perturbations that tended to drive the eyes in the same direction as the existing pursuit. Data from two other monkeys showed the same general effects (Fig. 4, D and E).

Ocular tracking of a target that moves together with a textured background: effects of brief perturbations of the background (paradigm 2)

We eliminated the background motion on the retina during pursuit in the period preceding the application of the background perturbation by moving the background together with the pursuit target. The brief perturbation was achieved by adding a rightward or leftward movement of 60°/s to the pre-existing background motion for 40 ms. Figure 5A shows the mean eye velocity responses of one animal to rightward perturbations of the background when that animal had been pursuing a target moving (with the background) at 0, 5, 10, and 20°/s rightward and leftward. Thus the conditions in Fig. 5A are the same as in Fig. 4A except that the background was stationary in the latter and moved with the background in the former, and there are two clear differences in the response profiles. When the background moved with the target, the effects of background perturbations showed less directional asymmetry, in part because the responses during rightward tracking showed less dependence on target velocity and in part because the responses during leftward tracking showed more dependence on tracking. Thus the responses to the perturbations were clearly very weak when the target was stationary and increased in magnitude with target velocity when the motions of the target and background during the perturbation were in the same or opposite direction, although the former was the more effective with a given pursuit speed. In this experiment, tracking performance was generally good at all target velocities so that the retinal slip velocity of the background during the perturbation was always very close to 60°/s. Similar modulatory effects were seen with leftward perturbations. To quantify these effects and allow easy comparison of the data from three animals, we expressed each as a percentage of the response when the target was stationary, exactly as we did for the data obtained with paradigm 1. These estimates of the percentage modulation are plotted in Fig. 5B, which shows that the responses to the background perturbation were enhanced regardless of whether the perturbations were in the same or the opposite direction to target motion especially at
high target speeds (20 °/s), although the effect was generally greater when the directions were the same. Similar effects were seen with the other two monkeys (Fig. 5, C and D). We also examined the effects of brief horizontal perturbations of the background when the animal had been pursuing a target moving at 20 °/s vertically together with the background. The effects were greater than during fixation but less than during horizontal pursuit (120 ± 30% modulation for upward pursuit, 150 ± 30% for downward pursuit).

Effect of restricting the perturbations to the central or peripheral retina

In one experiment, the random-dot pattern on the screen was partitioned into a circular central region, 15° across, and a surrounding peripheral region, permitting us to restrict the perturbations to the central or peripheral regions of the retina (see METHODS). Sample mean eye velocity profiles from one monkey in response to brief perturbations of the central and/or peripheral parts of the background (after the animal had been tracking the combined motion of the target and the entire background) are shown in Fig. 6. For the sample data shown, the initial motion of the target and background was always 20 °/s rightward and the perturbations were always 60 °/s rightward motion applied for 40 ms. During both fixation and pursuit, the responses to the perturbations were greatest when applied to the central region alone, weaker when applied to the entire background, and appreciably weaker when applied to the periphery alone (cf. Kawano and Miles 1986). Similar data were obtained for the opposite direction of motion and from another animal. We again normalized the data for each by
expressing them as a percentage of the response when the target was stationary and computed the means for the three animals. These estimates of the percentage modulation indicate that the responses to the background perturbation were always enhanced by the prior tracking, the percentage enhancement ($\frac{n}{H11005}$) being 436/90% (SD) when the perturbations were restricted to the center, 544/134% when applied to the entire background, and 417/275% when restricted to the periphery.

**FIG. 5.** Ocular tracking responses during pursuit of a target moving together with the background. A: sample average eye velocity profiles obtained from monkey 58, resulting from application of background perturbations (60 °/s, 40 ms, rightward) during pursuit of a target moving together with the background (5, 10, 20 °/s rightward, leftward; black lines) and during fixation (thick gray line). Thin gray lines show control traces (i.e., no applications of perturbations). Bar indicates period during which the perturbation was applied. B: percentage modulations of responses to rightward (closed symbols, continuous lines) and leftward perturbations (open symbols, discontinuous lines) for this monkey (58) are plotted against target velocity. C and D: percentage modulations for 2 other monkeys (C: 57, D: 59).

**FIG. 6.** Comparison of the effect of the background perturbation in the central and peripheral field. Sample average eye velocity profiles obtained from monkey 59, resulting from application of background perturbations (60 °/s, 40 ms, rightward) in central (thin line), peripheral (thick line), and both (dotted line) fields during rightward pursuit at 20 °/s or during fixation (bottom traces).

We were interested in the possibility that the prior existence of background motion on the retina was itself sufficient to alter the effects of subsequent perturbations of that background independent of pursuit per se. Thus we set up conditions in which the subject fixated a stationary spot while the background was moved and examined the ocular responses to a subsequent perturbation of those background images. Figure 7A shows sample mean eye velocity profiles obtained from one monkey when the background started moving at 20 °/s in the leftward (black line) and rightward (gray line) directions for 250 ms and changed to 40 °/s rightward for 40 ms—the transient perturbation—before resuming its original motion. The initial background motion resulted in some weak tracking, but this had largely subsided by the time the perturbation was applied. The two responses to the perturbation were dramatically different even though the retinal slip during the perturbations was almost identical, i.e., always within 1–2 °/s of 40 °/s. Thus the response to the perturbation was appreciably larger when it resulted in a reversal of the motion of the background (and its retinal image), so that the response to the perturbation after the background had been moving leftward was much greater than that after the background had been moving rightward. Using a range of initial background velocities (5, 10, 20 °/s, rightward and leftward) while keeping the background velocity during the perturbation constant at 40 °/s rightward indicated that there was a strong dependence on the prior velocity of the background. This dependence is shown in Fig. 7B (closed symbols, continuous line), for which plot we normalized the data by expressing them as a percentage of the response when the background was stationary (percentage modulation). In this graph, the percentage modulation showed a clear discontinuity at zero background velocity (cf. Fig. 3): when the prior background motion was leftward (negative in
so that the perturbation brought about a reversal of the background motion on the retina, the responses to those background perturbations showed a clear increase with increases in the prior background velocity; on the other hand, when the prior background motion was rightward (positive in Fig. 7B), so that the perturbation did not bring about a reversal of the background motion on the retina, the responses to those background perturbations were always very weak and showed little dependence on the prior velocity of the background. Similar data were obtained with leftward perturbations (open symbols, discontinuous line in Fig. 7B). The same effects were also evident in the data of two more monkeys (Fig. 7, C and D).

DISCUSSION

We studied ocular tracking responses of monkeys elicited by brief background motions (perturbations) in three prior visuomotor conditions. When the animal tried to pursue a moving target against a stationary textured background, ocular responses to the perturbations of that background were appreciable if the velocities of the target and the background during the perturbations were such that the target was overtaken by the background. On the other hand, if the velocities of the target and the background during the perturbations were such that the target overtook the background, the responses to those perturbations were very small. Furthermore, if the background moved together with the pursuit target—so as to effectively eliminate the reafference—the ocular responses to the perturbations showed less dependence on direction. In addition to them, we have demonstrated the effect of moving the background while the animal was fixating a stationary target. In this situation, the ocular tracking responses to subsequent brief perturbations of the moving background were appreciably weaker when the perturbations were in the same direction as the prior background motion than when in the opposite direction.

Comparison with previous studies

The influence of a moving background on the initiation of pursuit was studied on human subjects (Masson et al. 1995; Niemann and Hoffmann 1997; Schwarz and Ilg 1999) and on monkeys (Born et al. 2000). Both synergistic effects of the target and background motion (Masson et al. 1995; Schwarz and Ilg 1999) and their antagonistic effects were reported (Born et al. 2000; Niemann and Hoffmann 1997), probably depending on their experimental conditions. During the maintenance of pursuit, the effects of a stationary background were studied, and only a modest impact was reported (Collewijn and Tamminga 1984; Mohrmann and Thier 1995). In this study, we concentrated the effect of a background motion during the maintenance of the pursuit. Some previous studies demonstrated the ocular sensitivities to the retinal motion of the background during pursuit maintenance in humans. Suehiro et al. (1999), which is our earlier work, moved the background for a brief period (40 ms) when the human subject was pursuing a target. Schwarz and Ilg (1999) and Lindner et al. (2001) applied a longer background motion (200 ms) that starts in the initiation period of pursuit and covers a part of the maintenance period. Although the timing of the background motion was different, their results were consistent with that of Suehiro et al. (1999), i.e., eye velocity was increased when the pursuit and the background motion was in the same direction and was not altered or was changed only modestly when their motion was in opposite directions. In this study, we adopted the methods used by Suehiro et al. (1999) and demonstrated that monkeys
also showed the same direction selectivity in the response to a brief background perturbation during the maintenance of pursuit as in humans.

Miles et al. (1986) demonstrated that sudden motion of a large textured background initiated a tracking eye movement with an ultrashort latency (~50–60 ms), which they called “ocular following.” Gellman et al. (1990) showed that similar tracking eye movements could also be elicited in humans at a slightly longer latency (70–75 ms). The background motion stimuli used in this study were very similar to those used in the previous studies of ocular following and the perturbations generated responses with a similar ultrashort latency (~60 ms, see Figs. 1 and 2). This suggests that the perturbation responses observed here might be generated by the same or similar neural mechanisms as ocular following.

In addition to the experimental conditions used in our previous study on humans, we also used an experimental condition in which we asked the animal to attempt fixation of a stationary target while the textured background started to move (paradigm 3). In this condition, the initial background motion always resulted in some weak tracking in the direction of the background motion (see Fig. 7). However, Born et al. (2000) observed eye movements in the direction opposite to the background motion when their monkey tracked a target moving across a random-dot background started to move at the onset of the target motion. The differences might be due to the experimental conditions; Born et al. (2000) used a background of a low-density random-dot pattern (0.3%, whereas ours was high density (50%)), and asked the animal to make a saccade to an eccentric target (no saccade in our experiment).

Enhancement of ocular sensitivity to a background perturbation during pursuit

One of our remarkable findings is that the response to a background perturbation (in the same direction as pursuit in paradigm 1 and in both directions in paradigm 2) is larger during pursuit than during fixation of a stationary target (see Figs. 3–5). This property has been seen in humans (Suehiro et al. 1999). In our previous study, we have proposed that two mechanisms may be working when the subjects are pursuing a target moving across a stationary background. One of them is a generalized increase in the gain of visuo-motor processing for ocular tracking as a direct consequence of pursuit. The data obtained from the experiment of ocular tracking of a target that moves together with a textured background show that the responses to the background perturbations were enhanced regardless of whether the perturbations were in the same or the opposite direction to the target motion.

Schwartz and Lisberger (1994) showed that, during pursuit, there is an increased sensitivity to target motion. Their effects and our results share the following common features. 1) The effect was larger when the perturbations were along the axis of ongoing target motion (regardless of whether the perturbations were in the same or the opposite direction to target motion) than when the perturbations were orthogonal to the axis. 2) The gain of the response to the perturbation increased as a function of the target speeds. Although Schwartz and Lisberger (1994) suggested an increase in the gain of visuomotor processing for a pursuing target, our result from the experiment of restricting the perturbations to the central or peripheral retina suggests that the mechanism influences the efficacy of visual inputs well beyond the boundaries of the usual target spots, and that when subjects select a moving object to pursue, its motion would be boosted for visuo-motor processing irrespective of its size. Note that this property is also common in humans and monkeys (cf. Suehiro et al. 1999).

Evidence has been accumulated to understand the brain circuitry that initiates and maintains smooth pursuit eye movements, including the cerebral cortex, pontine nucleus, cerebellum, and brain stem (for recent review, Ilg 1997). Among these structures, Tanaka and Lisberger (2001, 2002) showed that the electrical stimulation in the frontal pursuit area (FPA) increased the ocular response to a brief perturbation of target motion and suggested that the FPA has a role in controlling the gain of the visuo-motor transmission for pursuit. This might explain a part of our findings, i.e., the enhanced responses to background perturbations observed here.

Selective insensitivity to the reafferent visual input

If there were any stationary background images beyond the boundary of the target, our first mechanism (i.e., the generalized increase in gain) might disturb the subject in tracking the target under the presence of stationary background. We have also proposed, in our previous work, the second mechanism that would rescue the subject from this problem. That is, the ocular tracking system reduces its sensitivity to the reafferent visual input when the animal is tracking a target across a background. We have observed similar direction selectivity in the responses to background perturbations during pursuit in paradigm 1 with that in humans (see Fig. 4). Thus the results from monkeys are consistent with this mechanism. We think that these two mechanisms are working together to sustain the pursuit eye movements against a stationary background in monkeys also.

The result from the experiment of attempting fixation of a stationary target seen against a moving textured background (paradigm 3), which is a new finding from this work, strongly suggests that the selective suppression does not require actual, massive eye movements but requires the existence of retinal slip of the background and/or relative motion between the target and background. An adaptive property of neurons on the sensory-motor pathway generating eye movements might be related to this selective insensitivity observed here. Lisberger and Movshon (1999) reported that neurons in the middle temporal (MT) area as a major source of the visual motion signal for ocular tracking showed adaptation for a step change in stimulus speed. Such adaptation in the MT area may decrease the responsibility to the motion inputs from the background in the same direction and therefore produce some part of the selective insensitivity to the reafferent inputs associated with pursuit.

Increase in the response during fixation against a moving textured background

In this study, we have also demonstrated that monkeys showed larger responses to background perturbations even during fixation when the background was moved in the opposite direction to the subsequent perturbation than when the background was stationary prior to introducing the background...
perturbation. As shown in Fig. 7, an optokinetic eye movement occurred in response to our conditioning motion of the background (i.e., sustained motion before the perturbation), and this optokinetic is less before the perturbation. Therefore in this situation, the animals canceled this eye movement to keep the eyes on the stationary spot to be fixated. To achieve this, the pursuit system of monkeys might be effectively working to cancel the optokinetic in this situation, if our second mechanism described above, i.e., a selective insensitivity alone, is not enough to suppress the optokinetic. If this is the case, the first mechanism we have described above, i.e., a generalized increase in gain of visuo-motor processing associated with pursuit, might be related to this enhancement, although the actual eye movement itself is very small. Note that the response to the background perturbation to the same direction as that of the conditioning would be suppressed by our second mechanism. However, it is still possible that the retinal motion of the background and/or the relative motion between the target and background may selectively increase the sensitivity to motion of the background toward the opposite direction (possible third mechanism). Schwartz and Lisberger (1994) showed that the response to perturbation of the fixation target, which was stationary before its perturbation, is affected in the presence of background motion at the time of the perturbation. The faster the background moved, the larger the response was. This similarity suggests that their and our findings may share a common mechanism. To clarify the mechanism underlying the findings, further systematic experiments are needed.

Is a monkey a good model of humans?

Although major properties of the responses to background perturbations during pursuit were common in humans and monkeys, there may be a minor difference. The magnitude of the responses to background perturbations in the direction of ongoing pursuit was generally larger when the monkeys were tracking a target against a stationary background than when they were tracking the target moving together with the background, while the responses in humans were quite similar in both situations (cf. Suehiro et al. 1999). This might be related to the property discussed in Increase in the response during fixation against a moving textured background, i.e., the enhancement based on the retinal motion of the background and/or the relative motion between the target and background. Humans may not have this property, whereas monkeys have it. This may be clarified by knowing the properties of the responses to background perturbations in paradigm 3 of humans. However, in the current step, we have shown that the major properties of the responses to background perturbations during pursuit are quite similar to those in humans, which were demonstrated by Suehiro et al. (1999). Thus two mechanisms that are purposeful for the pursuit in the presence of stationary background, which we proposed before, are consistent also in monkeys. Therefore we conclude here that a monkey is a good model animal of humans to investigate detailed neurophysiological mechanisms by which a stable pursuit is achieved even in the presence of stationary background.

ACKNOWLEDGMENTS

We thank Dr. F. A. Miles for valuable suggestions throughout this study. We also thank T. Furūhata and S. Inoue for secretarial assistance and T. Mega, A. Kameyama, and A. Muramatsu for assistance with animal preparation and maintenance.

GRANTS

This work was performed through the Advanced and Innovative Research Program in Life Sciences from the Ministry of Education, Culture, Sports, Science and Technology, the Japanese Government and was partly supported by the Cooperation Research Program of Primate Research Institute, Kyoto University.

REFERENCES


