Shift of Visual Fixation Dependent On Background Illumination

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Barash, Shabtai, Armenuhi Melikyan, Alexey Sivakov, and Michael Tauber. Shift of visual fixation dependent on background illumination. J. Neurophysiol. 79: 2766–2781, 1998. Visual fixation, the act of maintaining the eyes directed toward a location of interest, is a highly skilled behavior necessary for high-level vision in primates. In spite of its significance, visual fixation is not well understood; it is not even clear what attributes of the visual input are used to control fixation. Here we show, in four Macaca fascicularis monkeys, that the position the eyes assume during fixation depends on the luminance of the background. Dark background yields fixation positions that are shifted upward with respect to the fovea. Hence, if the background is dim, the eyes are positioned during fixation so that the target does not fall on the fovea. The size of the upshift remains almost unchanged while the eyes fixate at different orbital positions; thus the upshift is not caused by orbital mechanics. The upshift clearly increases with additional training in fixation with dark background, the upshift increases in size. The upshift is generated in extraocular muscle activation aimed to ‘‘home in’’ the eye on the target. What aspects of the visual input are used by this control process? Snodderly (1987) reported of the upshift varies between monkeys, for all monkeys the upshift is larger than the radius of the fovea. Hence, if the background is dark, the eye is directed above the target. With the head rotated with the head. The upshift increases gradually with decreasing levels of background luminosity. Luminosity, not visual contrast, is indeed the primary variable determining the size of the upshift. The contribution of a unit area of the retina to the upshift decreases as inverse square root of distance from the target; therefore, it is the perifoveal region of the retina that mostly contributes to the upshift, while the far periphery has little influence. The upshift can be induced or canceled in the midst of a fixation by changing the background illumination; hence, the upshift is indeed an attribute of the fixation control system. Finally, the fixation-upshift studied here is different from a previously reported upshift of the endpoints of memory-guided saccades with respect to their target locations. This consideration might explain the greater dispersion of fixation positions in the dark; however, it does not offer any insight as to the directionality of the upshift. Why does the fixation position always upward?

The fixation upshift is reminiscent of another type of upshift of eye position—the ‘‘memory upshift’’ that occurs during performance of memory-guided saccades. In this task, the monkey must make a saccade toward the remembered location of a peripheral target that was flashed some time before the saccade. (During the presentation of the target as well as during the subsequent memory interval, the monkey must maintain fixation of a central fixation spot). If the background is dark or dimly illuminated but featureless, the eye position at the completion of a memory-guided saccade is above the actual target position (Gnadt et al. 1991, White

INTRODUCTION

Maintaining visual fixation is a difficult motor control task (though often an belittled one). High-acuity vision is possible only if during fixation the eyes are directed at the object of interest almost without movement (reviewed Carpenter 1988; Leigh and Zee 1991). To restrict ocular mobility during fixation, extraocular muscle activation must balance out orbital tissue elasticity. Extraocular muscle activation must be very orderly and well coordinated, otherwise twitches and drifts will undermine immobility. Indeed, the eyes are not perfectly immobile during fixation; small eye movements can be discerned, including fixation-saccades, drift, and tremor (Skavenski et al. 1975). In spite of its obvious importance, control of visual fixation is not well understood. Even the existence of a separate fixation system, which is different from the pursuit system, was in doubt until relatively recently (Luebke and Robinson 1988). Fixational neuronal activity exists in many brain regions, but an overall view of the fixation system is lacking.

As a control process, fixation converts visual input into coordinated extraocular muscle activation aimed to ‘‘home in’’ the eye on the target. What aspects of the visual input are used by this control process? Snodderly (1987) reported of the upshift varies between monkeys, for all monkeys the upshift is larger than the radius of the fovea. Hence, if the background is dark, the eye is directed above the target. With the head rotated with the head. The upshift increases gradually with decreasing levels of background luminosity. Luminosity, not visual contrast, is indeed the primary variable determining the size of the upshift. The contribution of a unit area of the retina to the upshift decreases as inverse square root of distance from the target; therefore, it is the perifoveal region of the retina that mostly contributes to the upshift, while the far periphery has little influence. The upshift can be induced or canceled in the midst of a fixation by changing the background illumination; hence, the upshift is indeed an attribute of the fixation control system. Finally, the fixation-upshift studied here is different from a previously reported upshift of the endpoints of memory-guided saccades with respect to their target locations. This consideration might explain the greater dispersion of fixation positions in the dark; however, it does not offer any insight as to the directionality of the upshift. Why does the fixation position always upward?

The fixation upshift is reminiscent of another type of upshift of eye position—the ‘‘memory upshift’’ that occurs during performance of memory-guided saccades. In this task, the monkey must make a saccade toward the remembered location of a peripheral target that was flashed some time before the saccade. (During the presentation of the target as well as during the subsequent memory interval, the monkey must maintain fixation of a central fixation spot). If the background is dark or dimly illuminated but featureless, the eye position at the completion of a memory-guided saccade is above the actual target position (Gnadt et al. 1991, White
et al. 1994), as if the representation of the world in memory is shifted upward. It is important to determine the relationship between the memory-upshift and the upshift of visual fixation explored in the present work. Could these be two facets of the same mechanism? This question is particularly relevant because the anatomic substrate of the memory-upshift already has begun to be explored by Stanford and Sparks (1994), who suggested that the source of the memory-upshift is likely to downstream from the superior colliculus. If the same process lies at the basis of both types of upshift, then Stanford and Sparks’ results would apply directly to the fixation upshift explored here.

METHODS

Four M. fascicularis monkeys were prepared for experiments combining single-unit recordings and eye position measurements. These experiments are not part of the present study and will be described elsewhere. Because visual fixation is always the first step in training, these monkeys were adequate for the present study. All experimental procedures are standard and follow the National Institutes of Health guidelines and local regulations. Eye position was measured using the standard scleral search coil technique (Fuchs and Robinson 1966; Judge et al. 1980) and sampled by a laboratory computer at a rate of 500 samples/s, with a 16-bit resolution. Under general anesthesia [with pentobarbital sodium (Nembutal) as primary anesthetic], in sterile, aseptic conditions, monkeys were implanted with the scleral search coil and with a skull cap. The cap was made out of sterile orthopedic bone cement (CMW3, CMW Laboratories Dentsply, Blackpool, UK) attached to the skull by cortical bone screws (Aesculap, Tuttlingen, Germany). The cap contained a recording chamber, and a head post for immobilizing the head during experiments (Crist Instrument, Damascus, MD). Monkeys were monitored postsurgically and received antibiotics and analgesics as indicated.

Training was initiated after full recovery several weeks after surgery. After the monkeys accomplished adequate performance of the fixation task, three of the monkeys had extensive training on complex cognitive tasks before the present study was conducted. Neuronal recordings were performed in two of these three monkeys. During most of these training and recording sessions, visual stimuli had appeared over a dark background. In contrast, the fourth monkey participated in the current study beginning almost immediately after its training was started (days 4 and 5 of his training).

The fixation task is illustrated in Fig. 1. A trial begins when a small, circular target spot appears at an unpredicted position on a tangent screen, positioned 86 cm in front of the monkey. Target size was usually 0.2°, but sometimes 0.1 or 0.15°. The monkey had 1 s to enter an eye-position window centered at the location of the target. Usually the window is made small enough (1°–2°) to ensure that the monkey does fixate the target. In the present study windows were made much larger (5°–15°), so that shifted fixation would not appear as a fixation error. We verified that the monkey does fixate the target by monitoring the variability of fixation position. Almost without exception, the variability of fixation position remained small, much smaller than window size. The tight clustering of the fixation position of each target is shown in Fig. 2. The clusters of fixations of different targets are unequivocally separated; the geometric configuration of the fixation positions is the same as the configuration of the targets. (In the few instances in which fixation performance did begin to deteriorate, the experiment immediately was aborted and was replaced by a standard fixation task with illuminated background and small windows). Thus fixations did not become imprecise due to the usage of the larger window.

The monkey had to maintain his eyes within the fixation position window for 1.5 s. The mean eye positions, as presented in Fig. 2, were calculated from the 1-s intervals that had begun 0.5 s after the eyes had entered the window (the interval marked as 0–1,000 ms in the schematic trial of Fig. 1A). At this time, all correction saccades are over, and the eye safely can be presumed to be under the fixation control system. If the eye remained in the eye-position window for the required 1.5 s, the trial was declared a hit and the monkey was rewarded by an apple juice drop of 0.1–0.4 ml volume. If the eye went out of the window prematurely, the trial was aborted, declared an error, and the monkey was not rewarded. The error rate was generally low in this study, typically <5%. All figures and analyses are based solely on hits.

Targets were positioned in the 24 locations shown in Fig. 1B. Target locations were selected in a randomly interleaved order (1

FIG. 1. Experimental procedure. A: a schematic trial. A single dot of light (fixation target) appears on the screen; to obtain apple juice reward, within 1 s the monkey has to move his eyes into a fixation window surrounding the target and to maintain his eyes in the window for 1.5 s. Schematic eye position, thick trace; schematic window, dotted traces. Note a real trial is characterized by 2 such panels—one for the horizontal dimension, 1 for the vertical. Mean eye position, during the last 1 s of fixation, is taken subsequently to represent the mean fixation position of this trial. (Presumably all fixation movements are over by 0.5 s after entry into window). B: target locations. For clarity, targets not drawn to scale (actual target size much smaller). In each block of trials, targets appeared in the 24 locations that are shown in B, 10 or 20 trials per location.
FIG. 2. Demonstration of the upshift of fixation positions in 4 monkeys. Data of each monkey are represented on a separate panel. Each dot represents the mean eye position of a single trial, derived as illustrated in Fig. 1A. Red dots, trials with illuminated background; blue dots, trials with dark background. Note that the only difference between the red and blue trials is in the level of background illumination; target spots and procedure are identical. Note further that the target configuration, shown in Fig. 1B, is reflected separately in the configuration of the red clusters and the configuration of blue clusters. Blue clusters are shifted with respect to the red clusters in a roughly upward direction.

target per trial). Targets were arranged on three circles, usually of radii 5, 10, and 20° but sometimes of radii 5, 12.5, and 20°. Experiments were conducted in a fully light-tight room. Levels of luminance were measured using an optometer (model 161, United Detector Technology, Hawthorne, CA). Stimuli were presented on a tangent screen using a video projector (model 1208, Barco, Belgium) in a back-projection configuration. The projector was the only source of visible light—for both targets and background. With dark background, the illumination was within the noise level of the instrument (ca. 0.001 candelas/m²). The level we used for
targets in this study, which we will call bright, is 37 candelas/m\(^2\). The level we used for background, which we will call illuminated background, is 1.36 candelas/m\(^2\). These values were measured at the center of the screen; at the edges of the screen there is an attenuation of \(\sim 25\%\). In the experiment of Fig. 5C (see Dark background versus high visual contrast in RESULTS), the dim target was 3.5 cd/m\(^2\). In the experiment of Fig. 5B (see Graduality of the upshift) the luminance levels used for the background were: 0.006, 0.015, 0.083, 0.30, 0.71, 1.4, and 2.3 cd/m\(^2\).

The calibration of eye position was based on coil signal measurements during fixations with illuminated background. Eye position calibration must be carried out in the background level at which the fovea is directed at the target during fixation. Illuminated background is therefore probably appropriate for calibration (see DISCUSSION).

RESULTS

Mean eye position during visual fixation is shifted upward if the background is dark

We overtrained monkeys in memory-guided saccades and in related tasks while the visual background was dark. Dimly illuminating the background resulted in a disastrous deterioration in performance. The monkeys could not achieve even the initial fixation of the trial; yet in dark background, their performance remained almost perfect. To resolve this paradox, we directly compared fixations in illuminated versus dark background. Figure 1 illustrates the procedure; see METHODS for details. Figure 2 shows, separately for each of the four monkeys, the mean fixation positions for trials of two blocks, one block with illuminated background (red dots), the other block with dark background (blue dots). The only difference between the blocks is the background luminance; targets and behavioral procedures remain unchanged.

Each panel of Fig. 2 contains clusters of blue dots and of red dots. To each target location correspond both a cluster of blue dots and a cluster of red dots. Both the configuration of the blue clusters and the configuration of the red clusters replicate the three concentric-circles configuration of the targets, shown in Fig. 1B. However, the circles of blue clusters are shifted with respect to the circles of red clusters in a roughly upward direction. The size of this shift varies from one monkey to another, as illustrated in the different panels of Fig. 2. In all monkeys, however, the shift is so large that the red and blue clusters, that correspond to the same target, are segregated almost totally from each other.

Figure 3 illustrates quantitative analysis of the data presented in Fig. 2. Each red dot in Fig. 3, A–D, corresponds to a red dot in Fig. 2, that is, to a single fixation trial with illuminated background; similarly, each blue dot in Fig. 3, A–D, corresponds to a blue dot in Fig. 2, that is, to a fixation with dark background. Rather than displaying the absolute value of the eye position as in Fig. 2, Fig. 3, A–D, shows the displacements of eye positions from targets. This allows to pool together data from fixations of different targets. The 480 red dots in each panel are clustered together around the origin (the closer a dot is to the origin, the more precise was the fixation in the respective trial). In contrast, the 480 blue dots are clearly positioned away from the origin, roughly above it. The statistics, listed in Table 1, confirm the existence of a shift in the displacements’ vertical components. The mean of the vertical components of the blue dots is significantly more than zero for the four monkeys. The means of the vertical components of the blue and red dots are significantly different from each other (last line in Table 1). However, for three of the four monkeys, there is also a significant horizontal shift, though much smaller than the vertical. How precisely is the shift directed upward?

An alternative “vertical” axis may be defined for each monkey, as the line passing through the origin and the through the center of mass of the blue cluster of dots in Fig. 3, A–D. This axis and its orthogonal “horizontal” are plotted in green in Fig. 3, A–D. Figure 3, E–L, compares the displacements in illuminated versus dark backgrounds; the statistics are listed in Table 2. The horizontal and vertical components of the displacements are analyzed separately. Horizontal and vertical are applied here with respect to the green frames of coordinates. The means of the horizontal components thus defined, of both blue and red dots, are all zero. The means of the vertical components of the red dots are also very close to zero. Only the means of the vertical components of the blue dots are all significantly more than zero. The null hypothesis, that the means of the vertical components of the red and blue dots are equal, is rejected with significance 1 (\(P = 0\)) in the four monkeys. (More precisely, the \(P\) value is less than the level of precision of double-precision arithmetic in contemporary computers).

Thus each monkey can be assigned a frame of coordinates, rotated from earth vertical by a few degrees, in which the shift is purely “vertical” and always upward. These personal coordinate frames probably primarily reflect the monkey’s head position, which was not perfectly aligned with earth coordinates. Later we shall show that the shift rotates with the head; indeed, the almost perfectly vertical shift of monkey \(J\) was obtained by fine-tuning the position in which its head was fixed. Another factor that perhaps might affect the personal coordinate frame is the exact location of the dorsal rod peak (see DISCUSSION).

Shift is independent of orbital position

Another point that becomes evident immediately on examining Fig. 2, is that, for each monkey, the characteristic shape of a red-blue cluster pair, and the size of the shift in particular, is largely invariant of target position, hence of the position of the eye in the orbit. This invariance contrasts with the significant differences between monkeys. The upshift does depend to a small degree on the vertical component of the orbital position, the regression coefficients being \(-0.07, -0.04, -0.03,\) and \(-0.01\) in the four monkeys, respectively; that is, the upshift is somewhat smaller if the monkey is fixating targets in the upper parts of the field. Nevertheless in these locations, the shift remains as clear as anywhere. Therefore we conclude that the shift is a central effect, though it may be attenuated slightly by the elastic restoring forces of the orbit, which are directed downward for fixations of the upper parts of the field.

Repeatability and effect of experience

Figure 4 shows that the upshift can be repeatedly induced almost without change in size and direction. Each mark in
FIG. 3. Quantitative analysis of the upshift of fixation. A–D: displacements of fixation positions from targets. Each dot represents the vectorial difference of the mean eye position of a single trial (same data as in Fig. 2) minus the target position for that trial. Red dots, trials with illuminated background; blue dots, trials with dark background. Green frame of coordinates is defined to fit the shift between red and blue clusters of each monkey and probably primarily reflects the position in which the monkey’s head was fixated. E–L: histograms of the vertical and horizontal components of the displacements with respect to the green frames of coordinates. Each column of histograms belongs to the monkey listed at the top of the figure and describes the data illustrated in the scatter plot in the top of that column. Red histograms describe displacements with illuminated background; blue histograms, displacements with dark background.
Table 1. Displacement of fixation positions from targets

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Monkey 2</th>
<th>Monkey 3</th>
<th>Monkey 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark</td>
<td>0.036 ± 0.72</td>
<td>-0.30 ± 0.64</td>
<td>0.034 ± 1.01</td>
</tr>
<tr>
<td>Significance</td>
<td>0.28</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Light</td>
<td>0.00 ± 0.53</td>
<td>0.00 ± 0.35</td>
<td>0.05 ± 0.57</td>
</tr>
<tr>
<td>Significance</td>
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<td>1</td>
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</tr>
<tr>
<td>Rejection</td>
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<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Light vs. dark*</td>
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<td>0</td>
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<tr>
<td>Significance</td>
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<td>1</td>
<td>0.26</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Vertical</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark</td>
<td>4.3 ± 1.55</td>
<td>2.38 ± 0.66</td>
<td>1.27 ± 0.90</td>
</tr>
<tr>
<td>Significance</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Rejection</td>
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<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Light</td>
<td>0.00 ± 0.75</td>
<td>0.00 ± 0.69</td>
<td>0.08 ± 0.54</td>
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<tr>
<td>Significance</td>
<td>1</td>
<td>1</td>
<td>10^-3</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Light vs. dark*</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Significance</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Data relative to earth vertical. Values are means ± SD. Horizontal and vertical components in dark and light are separately tested against the null hypothesis of mean = 0. Then the horizontal and vertical components are directly compared, with null hypothesis that their means are equal. * Comparison is of means.

Fig. 4 represents the mean eye position, calculated for a block of 10 trials per target. The background illumination was alternated between blocks—illuminated background in the first block, dark in the second, illuminated in the third, and so on to the eighth block. The results are clear-cut: the fixation positions of the dark-background blocks almost coincide as do the fixation positions of the illuminated-background blocks. The two clusters of fixation positions are segregated clearly from each other. Thus the order in which the blocks are performed is insignificant, the upshift is precisely replicated. Indirectly, these results also show that the upshift is not an effect of a generalized deterioration of performance as, for example, in fatigue.

Although Fig. 4 settles the issue of replicability in the short time range, a different issue is whether the shift is modified over long periods. Monkeys 1–3 were investigated in the present study after many months of intensive training mostly with dark background. Could it be that the upshift has been shaped by this training?

To examine this issue, we asked whether the upshift exists in a naive, newly trained monkey. The data illustrated in Fig. 2 for monkey 4 was collected at the end of the first

Table 2. Displacement of fixation positions from targets

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Monkey 2</th>
<th>Monkey 3</th>
<th>Monkey 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark</td>
<td>0.47</td>
<td>-7.3</td>
<td>14.9</td>
</tr>
<tr>
<td>Significance</td>
<td>0.00 ± 0.72</td>
<td>0.00 ± 0.65</td>
<td>0.00 ± 0.995</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Light</td>
<td>0.00 ± 0.53</td>
<td>0.00 ± 0.37</td>
<td>0.02 ± 0.55</td>
</tr>
<tr>
<td>Significance</td>
<td>1</td>
<td>1</td>
<td>0.26</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>No</td>
<td>No</td>
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<tr>
<td>Light vs. dark*</td>
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<td>0.59</td>
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</tr>
<tr>
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<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Vertical</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark</td>
<td>4.31 ± 1.55</td>
<td>2.40 ± 0.65</td>
<td>1.31 ± 0.91</td>
</tr>
<tr>
<td>Significance</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rejection</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Light</td>
<td>0.00 ± 0.75</td>
<td>0.00 ± 0.68</td>
<td>0.091 ± 0.57</td>
</tr>
<tr>
<td>Significance</td>
<td>1</td>
<td>1</td>
<td>10^-3</td>
</tr>
<tr>
<td>Rejection</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Light vs. dark*</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Significance</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Data relative to rotated coordinates. Values are means ± SD. Horizontal and vertical components in dark and light are separately tested against the null hypothesis of mean = 0. Then the horizontal and vertical components are directly compared, with null hypothesis that their means are equal. * Comparison is of means.
To test this alternative hypothesis, we have repeated the experiment of Figs. 2 and 3 in the presence of a large, bright rectangle, positioned in the periphery of the visual field. If the alternative hypothesis is valid, then the presence of the rectangle should be sufficient to cancel the upshift, regardless of background illumination. Figure 5A shows, however, that the upshift is preserved in the presence of the peripheral rectangle. Thus prominent visual features in peripheral visual field do not abolish the upshift. The upshift must be determined by the background illumination within some immediate neighborhood of the target.

Graduality of the upshift

Is the upshift all-or-none or gradual? Is there some threshold level for background luminosity, above which there is no upshift and below which the upshift is fully expressed—or, alternatively, does the upshift gradually increase for darker levels of background illumination? This issue is taken on in the study illustrated in Fig. 5B, which shows mean fixation positions for single fixation trials with seven background illumination levels (see METHODS for exact values). Three trials are presented per each illumination level for each target location. The background illumination levels are color coded: deep blue represents dim background, red represents brightly illuminated background. Figure 5B shows that the size of the upshift is a gradual function of background illumination. Dimmer background yields a larger upshift.

Dark background versus high visual contrast

Many phenomena in visual perception are determined not by the absolute level of luminosity but by visual contrast. Indeed, all previous results can be explained in terms of the contrast between target and background: because target illumination was the same for dark- and illuminated-background blocks, dark-background blocks can be viewed as “high-contrast,” whereas illuminated-background blocks as “low contrast.” The null hypothesis of this study is, thus, that the upshift is caused by high contrast between target and background not by absolute background luminosity.

The study illustrated in Fig. 5C explores this issue. Would there be upshift if the background is dark, even if the target is dim, hence the contrast is low? The first two blocks illustrated are the same as before. Blue dots represent fixation positions obtained with bright targets positioned over dark background. Red dots represent bright targets over illuminated background. The green dots represent trials of the test block. They were obtained with dark background but very dim targets. In fact, the target luminosity was set just above threshold—in the sense that dimmer targets did not consistently evoke a fixating response by the monkey (see METHODS for luminosity). Hence green dots represent dark background but lower visual contrast.

The results are, again, clear. The green dots overlap the blue dots, and both are totally segregated from red dots. Quantitatively, the upshift for the green dots is $4.79 \pm 0.87^\circ$, for the blue dots $4.65 \pm 0.64^\circ$. (These numbers are for the data illustrated in Fig. 5C). These numbers are very similar, the difference not statistically significant. Hence, the null hypothesis is rejected; the upshift is caused by dark background, not by visual contrast.
FIG. 5. Controls and ramifications. A: control for screen edges: screen edges can be viewed in illuminated background, but not in dark background. Replication of the experiment of Fig. 2 in the presence of a bright rectangle in the far periphery (in the position illustrated in the figure). That is, red dots are the mean fixation positions for trials in which the visual stimulus was target, illuminated background, and the rectangle; blue dots, fixation positions for trials with identical target and rectangle, but the background is dark. Rectangle dimensions, 70 \times 55^\circ, luminance bright, same as target. B: upshift is a gradual function of eye position. Mean fixation positions for short blocks with 7 background illumination levels (see METHODS for values). Short blocks, 3 trials per target position per block. Seven levels of background illumination are color coded, from dark (deep blue) to illuminated (red dots). C: upshift is determined by the background luminosity not the contrast. Mean fixation positions for 3 blocks of trials. Blue dots, dark background, bright targets. Red dots, illuminated background, bright targets. Green dots, dark background, dim targets (just above threshold). Hence green dots represent dark background but lower contrast. Green and blue clusters overlap. D: upshift rotates with the head. Red dots, illuminated background. Blue dots, dark background, head tilted 8° counterclockwise. Green dots, dark background, head tilted 11° clockwise. Green and blue clusters are well segregated (compare D with C) and rotated in opposite directions.
Spatial coordinate frame: head-centered

What is the spatial framework ("coordinate system") in which the upshift is coded? Is it with respect to the eye, head, and trunk or to earth vertical? To examine this issue, we have repeated the measurement of the upshift—while the head was fixed slightly tilted, in two angles. We wish to emphasize that our experimental setup does not allow us precise measurement of head position. The head was rotated only with respect to the occipito-nasal axis not with respect to the interaural axis, and the angle of the head with respect to earth vertical was estimated by measuring the line passing through both eyes. Therefore, the results should be taken with caution. Nevertheless, the overall pattern of the results are clear. Figure 5D shows two sets of dots obtained in the dark: the green dots were obtained with the head tilted −11° clockwise; the blue dots with the head tilted −8° counterclockwise. The red dots, as usual, represent fixations with illuminated background, which were well aligned for the two head positions.

The blue and green clusters are well segregated and are roughly symmetric with respect to the vertical meridian. Indeed, numerically, the tilt of the upshift is seen to be very similar to the tilt of the head. For the blue dots, the mean horizontal shift was −0.52 ± 0.39°, and the mean vertical shift 2.77 ± 0.93°. Thus the mean angle of the shift of the blue dots is 10.7°—similar to the 8° tilt of the head. Similarly for the green dots, the horizontal shift was 0.76 ± 0.44°, the vertical shift 3.2 ± 0.87°, that yield a mean tilt angle of 13.3° for the upshift—similar to the 11° tilt of the head.

The eyes and the head are not perfectly aligned. They are separated by the ocular counterrole, which in principle can be used to determine whether the shift is oculo-centric or craniocentric. However, counterrole is typically only 10° of the head tilt (for review see Carpenter 1988; Leigh and Zee 1991) and is therefore beyond the resolution of our current study. Also, our coils are inadequate for recording ocular torsion. Therefore we cannot decide if the shift is with respect to eye or head. However, in light of the segregation of the green and blue dots, we can reject the hypothesis that the shift is determined by earth vertical.

Size of retinal region contributing to upshift

The control study presented in Fig. 5A showed that even a brightly illuminated large rectangle has little effect on the upshift if it is confined to the far periphery of the visual field. Therefore, the level of illumination in some limited region around the line of gaze determines the upshift. How large is this region? Is there indeed a discrete region over which the upshift is determined or does the contribution a unit area in the retina gradually fall down with eccentricity? The experiment presented in Fig. 6 obtains first data directed at this issue. Figure 6A shows the stimulus used in this study. A fixation spot appears at the center of the screen. It is surrounded by a dark circle; the region of the screen distal to this dark circle is set to the standard illuminated background. The radius of the dark circle can be any one of a small set of predetermined values, presented in a randomly interleaved manner. The monkey is requested to fixate the central spot. For each trial, the mean fixation position is obtained in the usual manner.

The results are presented in Fig. 6B. The upshift is a roughly linear function of the radius of the dark circle. This, in fact, shows that the contribution of a retinal unit area to the upshift decreases with eccentricity as the inverse of the square of eccentricity.

Changing the background illumination during fixation causes changes in the eye position

Although we have claimed from the outset that the upshift is related to the control of fixation, this claim requires substantiation. In particular, Snodderly and Kurz (1985) found that most of the variation in fixation position is in the intertrial differences rather than within trials. Should the upshift actually be attributed to the saccadic movement that brings the eye to the target at the beginning of the trial rather than to the fixation itself? To directly test this alternative, we have performed the following experiment. There were two types of trials at a randomly interleaved order. One type was the standard fixation trial. The fixation target always appeared at the straight-ahead direction, and the monkey had to maintain fixation for 4.5 s. Background was illuminated (also during intertrial intervals). The second type of trials began in just the same manner. However, after 1 s of fixation, the illumination of the background was turned off for 2.5 s; at the end of which, the background became, again, illuminated. The fixation target was maintained without a change throughout this period. Now, if the upshift is an attribute of the fixation control system, we would expect the vertical component of the eye position to ascend after the darkening of the background and descend back to the baseline level after the reillumination of the background. If, however, the ‘null’ hypothesis holds, namely, the upshift is an attribute of the saccades that bring the eye to the target at the beginning of the trial, then eye position should not be influenced by midfixation changes of background illumination.

Figures 7 and 8 show the results. Figure 7 shows the mean fixation position (±SD) throughout the two types of trials. A block of 75 trials of each of the two types was used for the figure. The thick trace of Fig. 7A shows the mean vertical component of the fixation position in trials of the first type,
FIG. 7. Upshift is an attribute of the fixation control system: changing the background illumination in the midst of fixation causes the upshift to appear and disappear. In this block, targets appeared at the center of the screen, with illuminated background, for 4.5 s. In half the trials (randomly interleaved), after 1 s of fixation, the background became dark for 2.5 s. A: vertical component of trials in which the background was turned off and then back on. Thick trace, mean eye position, thin traces, 1 standard deviation range from the mean position. Seventy-five trials. Dotted vertical lines, time of background illumination offset and subsequent onset. B: similarly, vertical component of fixation position for the 75 trials in which the background remained illuminated. C: horizontal component of fixation position for same trials as in A. D: horizontal component of fixation position for same trials as in B.

and the thin traces surrounding the thick trace mark the coincident SD eye-position interval. The offset of the background is marked by the dotted vertical line on the left. After the offset of the background, almost without exception, the monkey made a small fixation-saccade directed upward. This fixation-saccade initiates the upshift. Figure 7C, the coincident horizontal component, is almost flat at the time of the first fixation-saccade—hence, the first fixation-saccade is directed indeed almost perfectly upward. As the fixation with dark background continues, the vertical component of the fixation position remains above baseline as long as the background remains dark. Shortly after the background is illuminated (marked by the second dotted vertical line), the mean fixation position rapidly descends back to the baseline level. The return of the fixation position to baseline probably also involves fixation-saccades. After the return to baseline, the variability of the fixation position is also reduced to about the initial level. Figure 7B and D, shows the analogous traces for the fixation position, computed for trials of the second type, in which the background remains illuminated. The fixation position remains close to the position of the target throughout the trial. The difference between the vertical components of the fixation positions in the two types of trials—between A and B of Fig. 7—is striking. Remember, further, that these trials were collected in the same block. The difference between the two panels confirms that the changes in fixation position illustrated in Fig. 7A indeed result from the changes in background illumination.

Figure 7 shows that the transient emergence of the upshift,
There are two points to notice. First, at least in these trials, fixation-saccades are involved in both the generation of the upshift and in its abolishment. Second, during fixation with dark background, while the eyes are directed above the target, frequently the eyes make a fixation-saccade toward the target, followed briefly by a second fixation-saccade back to a position above the target. These brief fixations (separating the 2 fixation-saccades) can either reach the target (top) or fall short of it (2nd and 4th traces from top). Upward-going brief deviations of gaze occur, too (top), but they are less frequent than the downward deviations, which are directed toward the target. Pairs of closely timed fixation-saccades of opposite directions have been noticed by several investigators (Bahill et al. 1975; Skavenski et al. 1975; Snodderly and Kurtz 1985; van Gisbergen et al. 1981). The saccade pairs of Fig. 8 are reminiscent of the pairs described in these studies, although the time between the saccades here might be slightly longer (normally $>100$ ms). The more important difference is that here the saccade pairs seem directly related to visual function. It is as if the monkey is aware that he is not fixating the target, and therefore, occasionally, he looks toward the target, but then his eyes are turned away, upward, as if they are pooled away by a powerful, hidden force.

Fixation upshift, studied here, is different from the memory-upshift, of the end points of memory-guided saccades

The phenomenon described in the present paper is reminiscent of another type of upward shift of eye position, mentioned in the introduction: memory-guided saccades—that is, saccades made in the dark toward the remembered locations of previously flashed targets—end above the locations in which the targets were flashed (Gnadt et al. 1991, White et al. 1994). Figure 9B explores the relationship between the two types of upshift. The figure presents eye-position trajectories recorded while the monkey performed memory-guided saccades. Trials were made with featureless, illuminated background (red dots) and with dark background (blue dots). The figure shows superimposed trajectories of 10 trials per target position for each background illumination level. Each dot represents the position of the eye during a single sample; consecutive samples are 2 ms apart.

Two observations can be made in regard to Fig. 9B. First, both red and blue trajectories corroborate the existence of the memory-upshift reported by Gnadt et al. (1991). More specifically, downward movements are shorter than upward movements. Similarly for oblique movements, left-and-up directed saccades have a larger vertical component (but a similar horizontal component) to left-and-down directed saccades. (Oblique saccades made to the right hemispace show a similar asymmetry). Saccades directed toward targets on the horizontal axis (either leftward or rightward) are made in a direction above the horizontal axis. In sum, for illuminated, featureless background, memory-guided saccades in all directions end above the actual locations of their targets.

The question whether the two types of upshift result from the same neuronal process cannot be directly addressed on a behavioral level. We approached this question by asking,
FIG. 9. Further ramifications. A: fixation upshifts increase with training. Comparison of the upshift of monkey 4 at the 1st week of training and after 8 mo of training in fixation and other oculomotor tasks (e.g., memory-guided saccades). Same general format as Fig. 2. Blue dots, mean fixation position of 10 dark-background trials in the 1st week of training. Green dots, mean fixation position of 10 dark-background trials after 8 mo. Red dots, mean fixation position of illuminated-background trials, 10 trials per target in the 1st week and another 10 trials per target after 8 mo. B: upshift of the fixation position studied here is different from the previously reported upshift of the end points of memory-guided saccades with respect to their target locations. Trajectories of memory-guided saccades made to 8 target locations that are positioned on a 15° circle centered on the location of the initial fixation spot, at the center of the screen. Each dot represents a single eye-position sample; samples are 2 ms apart. Red dots, trials made with illuminated background; endpoints of saccades are shifted upward with respect to target locations. Blue dots, trials made with dark background; both initial fixation spot and memory-guided saccade endpoints are shifted upward with respect to the red trajectories by about the same magnitude. Hence the 2 shifts add up to each other.

Instead: can the two types of upshift add up to each other? The rationale is that if the two upshifts do result from a single neural process, in conditions in which both upshifts are maximal, the size of the upshift induced by both types acting together should be similar to the size produced by either type separately. Consequently, a common neural mechanism leads to the following predictions: the initial central fixation would show fixation upshift (blue dots would be positioned above the red dots) and in contrast, the eye positions at the completion of the saccades would be largely invariant of background illumination (red and blue end points would overlap).

Observation of Fig. 9B immediately shows that this prediction fails. On the contrary, the blue traces are shifted uniformly to above the red traces; the blue and red groups of trajectories are almost congruent to each other. Thus the fixation upshift and the memory-upshift add up to each other. Therefore, the two types of upshift are probably generated independently of each other.

DISCUSSION

Summary of the results

We have presented here evidence corroborating the observation of Snodderly (1987) that the position that the eyes assume, during fixation of a small target on a featureless background, depends on the illumination of the background. Namely, dark background yields fixation positions that are shifted upward with respect to the fixation positions obtained with an illuminated, featureless background. This upshift occurs even though the target spot is identical in the two cases. The upshift was measured in four M. fascicularis monkeys, and it was found to be highly reproducible and statistically significant beyond any reasonable doubt.

Having convinced ourselves that the upshift does exist, that it is not an artifact nor a reflection of a directionally nonspecific reduction in the precision of saccadic movements, we proceeded to explore its basic properties. The upshift is caused by control processes in the brain not by orbital mechanics. The upshift exists in naive monkeys, but with long intensive training it becomes more prominent. The upshift is a gradual effect not all or none: darker background generally yields a larger upshift. The upshift is determined by the luminosity of the background not by the visual contrast between target and background. The upshift is determined with respect to the eye or head not with respect to earth vertical—if the head is rotated relative to its naso-occipital axis, the shift rotates roughly with the head. The upshift is determined primarily by the retinal region close to the fovea; more specifically, the contribution of a retinal unit area de-
creases with eccentricity as the inverse square of eccentricity. Indeed, the upshift is truly an attribute of the fixation control system: it can be induced and abolished in the midst of fixation by changing only the background illumination. In these circumstances, both emergence and abolition of the upshift involve fixation saccades; the involvement of drift is less clear. During the upshifted fixations, the monkey occasionally makes saccades downward, toward the fixation target, but then briefly back to a position above the target. Finally, the fixation-upshift studied here is different from the memory-upshift reported by Gnadt et al. (1991). Indeed, the two types of upshift add up to each other.

A highly developed fovea is among the chief characteristics of the primate visual system. Efficient usage of the fovea depends on the precision of saccadic eye movements and of the fixations separating saccades. It therefore may be surprising that the control of fixations and saccades depends not only on complex features of the stimulus but on a "primitive" attribute such as the background light intensity.

**Upshift or downshift?**

An alternative explanation for our results could in principle be that fixation is precise if the background is dark and shifted downward to a position below the target if the background is illuminated. In our minds, it is by far more likely that fixations are precise in illuminated rather than in dark background. One reason is that illuminated background yields clusters of fixation positions that are both denser and more precise (Figs. 2 and 3 and Tables 1 and 2). Another reason has to do with the pattern of eye movements that frequently occur in the dark in which the monkey occasionally makes brief, back-to-back saccade pairs toward the non-shifted target (Figs. 8 and 9).

**Phylogenetic extent of the phenomenon of the fixation-upshift**

Next, we discuss several questions relating to the validity and extent of the phenomenon of the upshift. The first question is whether the upshift is species-specific, limited to *M. fascicularis* monkeys or does it exist also for rhesus monkeys and humans? As for humans, Snodderly (1987) reports that there is no fixation-upshift in humans. Clearly, this conclusion is representative of Snodderly’s data. But it is not absolutely obvious to us that there may not whatsoever be conditions in which humans would show a fixation upshift. First, although Snodderly managed to minimize task differences between monkeys and humans (one of Snodderly’s human subjects was trained nonverbally just like the monkeys), one difference between monkeys and humans occurs in many studies and probably does exist also between our monkeys and Snodderly’s human subjects. It concerns the amount of training. Our monkeys make thousands of fixation and saccade trials each day for long periods. This is much more training than human subjects usually would have. Amount of training is important: our *monkey 4* had a smaller upshift in his first week of training. Even at that stage he probably had had more training than Snodderly’s human subjects. Second, the “rod hot-spot,” which might be an anatomic analogue to the upshift (see further text), exists not only in monkeys but also in humans. These considerations lead us to question whether the total absence of upshift in humans is conclusive—even though Snodderly clearly shows that, in the basic condition, the fixation upshift is absent in humans.

The question whether the upshift exists in *M. mulatta* is interesting for two reasons. Absence of the fixation-upshift in *M. mulatta* would be surprising from an evolutionary perspective—due to the phylogenetic proximity between *M. fascicularis* and *M. mulatta*, which both belong to the *M. fascicularis* species group (e.g., Napier and Napier 1985).

On the other hand, upshift in *M. mulatta* monkeys is relevant for the many neurophysiological investigations of vision and eye movements performed in this species. Motter and Poggio (1984) compared eye position variability in fixating rhesus monkeys with dynamic noise versus blank, dim background. They report a slightly decreased variability for the dynamic noise background. The mean luminance of the display was probably higher for the random noise than for the blank state. Thus Motter and Poggio’s data may suggest that their rhesus monkeys also had an upshift. Further, Motter and Poggio, like Snodderly and Kurtz (1985) in *M. fascicularis*, found more variance in the vertical component of the eye position than in the horizontal component. Nevertheless, unequivocal answers will be obtained only by repeating in rhesus the experiments of the present study.

**Can monkeys be trained specifically not to upshift?**

We cannot at present answer this question with confidence because we have not explored it systematically. Some indirect evidence suggests that the capacity to learn to shift is limited at least. We rediscovered the fixation-upshift while trying to train monkeys to fixate in illuminated background, using shifted eye-position windows, derived from fixation in the dark. Snodderly (1987) reports having originally discovered the upshift in similar conditions. Our (and, apparently, Snodderly’s) failure to get the monkey to fixate the shifted windows may be taken to suggest that training to shift fixation is at least not generally easily possible.

It is important to realize that even if monkeys would eventually turn out to be able to learn not to upshift, this result would not “explain away” the phenomenon of the fixation-upshift, which emerges spontaneously in normal conditions, as we showed in this paper. In analogy, humans can be trained to reduce the frequency of fixation-saccades (Steinman et al. 1967, 1973). Surely no one would claim that this observation means that fixation-saccades do not exist!

**Is the fixation-upshift a result of the specific behavioral task we used, which does not explicitly require foveation?**

We did not request our monkeys to perform a specific task that intrinsically requires foveation, such as detection of subtle dimming (Wurtz 1969). Would the usage of such a task have prevented the upshift? Snodderly (1987) did apply a demanding, near-threshold spot-dimming foveation task but had observed the upshift nevertheless. Therefore the absence of a specific foveation requirement is not the cause of the upshift. It is worth noting that even if it were not for Snodderly’s results, the lack of foveation task hardly
can explain the fixation-upshift because of its directionality. Namely, absence of perfect foveation requirement could have explained a greater dispersion of the fixation positions, but—as far as we can see—would not have offered any insight why the center of the cluster of fixation positions is displaced from the target by several degrees, always in the same direction.

Explaining the upshift in terms of visual capabilities?

We now turn to possible explanations of the upshift. There seem to be two possible (noncontradicting) lines of explanation. The first has to do with visual capabilities; the second with oculomotor control.

In the present section, we consider the hypothesis that the upshift is a functional consequence of the nonuniform distribution of rods in the retina. It is conceivable that the dark background sets the visual system to an overall scotopic state in which there is not much sense to cover the target by the fovea because of its reduced sensitivity. Why, however, is the upshift always directed upwards? An anatomical prediction that would explain this directionality would be that there is a confined region in the retina, dorsal to the fovea, which has preferred visual capacity for scotopic vision.

Surprisingly, such a region does exist! Detailed quantitative mappings of cone and rod distributions in the retinas of *M. mulatta* and *M. nemestrina* (Curcio and Allen 1990; Packer et al. 1989; Wikler and Rakic 1990; Wikler et al. 1990) have come up with similar results. The same picture also holds for the dopamine-containing amacrine cells (Mariani et al. 1984). The highest density of rods is generally in an annulus that surrounds the fovea, called the “rod ring”; but, within the rod ring, rod density is not uniform. It is higher in the superior retina. The region of highest rod density is called “dorsal rod peak” or “rod hotspot.” It is located on, or close to, the superior vertical meridian. The eccentricity of the rod peak varies between individuals but it is generally >2 mm away from the center of the fovea. Therefore, the upshift is not an act of directing the dorsal rod peak, rather than the fovea, to the target. Nevertheless, for any eccentricity outside the foveola, there are more rods on the superior vertical meridian than on the inferior (Packer et al. 1989). The rod/cone density curve is steeper in the superior vertical meridian than in the inferior (Wikler et al. 1990). These observations suggest the hypothesis that the monkey’s strategy is to direct the visual axis toward a point in the superior retina that is intermediate between the fovea and the rod peak. Although the method by which the specific intermediate point is selected remains unclear, this hypothesis is consistent with the gradual increase in the upshift as a function of descending background luminosity. It is also consistent with the increase in upshift that comes with practice. Finally, because the dorsal peak is not perfectly aligned with the vertical meridian for all individuals, some of the scatter in the direction of the upshift (Fig. 3) could in principle be related to the precise direction of the dorsal peak in each monkey. (This does not contradict the suggestion made later that the primary source for the mismatch in direction with earth vertical is the posture of the head).

Crawford (1977) also provides supporting data for this hypothesis. Crawford qualitatively estimated that the proximal margins of the rod ring are closer to the center of the fovea in the superior direction than in the inferior. He further found by psychophysical measurements in rhesus monkeys that the sensitivity of the dark-adapted retina to weak, scotopic flashes is higher in the upper 2° than in the lower. These findings are consistent with the assumption that the upshift subserved a visual function. However, because eye position was not explicitly measured in this study, it is not perfectly clear to us that there was no interaction between upshift and sensitivity in these measurements. Although the analogy between the nonuniform rod density and the upshift is (for us) attractive, by itself it does not constitute an explanation for the upshift. The proportion by which there are more rods in the superior retina than in the inferior (30–50%) is not nearly as sharp as the proportion of trials in which the shift is directed upwards (nearly 100%). The same holds for the differences in processing the upper and lower hemifields by the visual cortex (Burkhalter et al. 1986; Felleman and Van Essen 1991). Under the influence, perhaps, of the asymmetries in both rod distribution and cortex, there seems to have emerged an independent active mechanism that drives the eye always upward while fixating in dark background.

Explaining the upshift in terms of the fixation-control mechanism

The second type of explanation for the upshift is in terms of the fixation control mechanism. We will consider four brain regions and speculate on the possible reflection in these regions of the directional asymmetry of the upshift. There exist examples of asymmetry in oculomotor control between horizontal and vertical and between up and down (for example, Grasse and Lisberger 1992; Schlykow a et al. 1996).

What brain regions are involved in the upshift? There seem to be essentially two criteria. The first is that many neurons in the candidate region would have fixational activity. Moreover, the region should not be too remote from the level of the oculomotor plant, for it is presumed to be involved in on-going control of fixation.

The second criterion is that the neurons of the region also would have visual activity. The upshift is clearly the outcome of sensorimotor integration: control of eye position is modulated by the sensation of background illumination.

The preoculomotor centers seem, at first sight, likely candidates. They satisfy the first criterion. The rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) and the interstitial nucleus of Cajal (INC) particularly are involved in vertical saccades and in the vertical component of fixation (Buettner et al. 1977; King and Fuchs 1979; Vilis et al. 1989; reviewed Leigh and Zee 1991; Sparks and Mays 1990). The anatomic separation of the vertical and horizontal components is attractive for explaining the confinement of the shift to the vertical dimension. However, the preoculomotor centers do not satisfy our second criterion: they are not usually considered to have visual responses.

The cerebral cortex might be too remote from the oculomotor plant to fully satisfy our first criterion. Other than that, some cortical regions are appropriate candidates. For example, in the parietal cortex there are strong fixational
activity, visual responses and also saccadic activity (e.g., Barash et al. 1991a,b). Moreover, a simple hypothesis could be offered regarding the way the upshift would be integrated in the gain-field coding scheme of area LIP (Andersen et al. 1990): gain fields simply would be shifted slightly as a function of background illumination. This hypothesis could be tested easily.

The cerebellum directly innervates the preoculomotor centers, and it also has visual responses. Cerebellar lesions result in inability to maintain eccentric gaze positions (Zee et al. 1980). Bicuculline injections into the fastigial nucleus result in a gaze deviation directed upwards (Sato and Noda 1992). Clinical evidence also suggests that the cerebellum may be involved in the upshift. Hotson (1982) showed changes in fixation saccades in cerebellar patients. Perhaps most interesting is the description by Zee et al. (1980) of a rare cerebellar pathological ocular sign. When their patient tried to maintain fixation in a lateral position, her eye would drift upward. This suggests cerebellar involvement in at least some up-down asymmetries.

However, the most promising location for recording experiments related to the upshift seems to us to be the superior colliculus. One reason for our preference is the established collicular polar map of saccade target direction (reviewed by Sparks and Groh 1995). In the rostral end of the colliculus, corresponding to the origin of the collicular map, there is abundant fixational rather than saccadic activity (Munoz and Guitton 1991; Munoz and Wurtz 1993a,b). Moreover, there is mutual inhibition between this zone and saccadic cells elsewhere in the colliculus.

Where would we expect activity to occur in the superior colliculus in the condition of upshifted fixation? Our hypothesis is that the upshift would yield a seemingly paradoxical pattern of activation. The fixation cells in the rostral pole would be active. (Munoz and Wurtz showed that these cells continue to discharge if the fixation stimulus is briefly blinked off.) However, contrary to normal fixation, visual responses will not also occur at the rostral pole because there is no visual stimulus at the line of sight; rather, visual stimulation would occur at another location of the colliculus, a location corresponding to a downward direction—opposite to the upshift. Bearing in mind the mutual inhibition Munoz and Wurtz found (see earlier text), this hypothesized pattern of collicular activation may explain the appearance of the saccade pairs briefly directed at the target, illustrated in Fig. 8. More specifically, this activation, if found, would explain the first saccade of the pair, directed toward the target; the force driving the second saccade, that recreates the upshift, would require further clarification.

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REFERENCES


