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Effect of Saccadic Adaptation on Localization of Visual Targets

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Awater, Holger, David Burr, Markus Lappe, M. Concetta Morrone, and Michael E. Goldberg. Effect of saccadic adaptation on localization of visual targets. *J Neurophysiol* 93: 3605–3614, 2005. First published December 22, 2004; doi:10.1152/jn.01013.2004. Objects flashed briefly around the time of a saccadic eye movement are grossly mislocalized by human subjects, so they appear to be compressed toward the endpoint of the saccade. In this study, we investigate spatial localization during saccadic adaptation to examine whether the focus of compression tends toward the intended saccadic target or at the endpoint of the actual (adapted) movement. We report two major results. First, that peri-saccadic focus of the compression did not occur at the site of the initial saccadic target, but tended toward the actual landing site of the saccade. Second, and more surprisingly, we observed a large long-term perceptual distortion of space, lasting for hundreds of milliseconds. This distortion did not occur over the whole visual field but was limited to a local region of visual space around the saccade target, suggesting that saccadic adaptation induces a visuo-topic remapping of space. The results imply that the mechanisms controlling saccadic adaptation also affect perception of space and point to a strong perceptual plasticity coordinated with the well-documented plasticity of the motor system.

INTRODUCTION

Human spatial visual perception is ordinarily veridical and accurate. However, humans dramatically mislocalize objects flashed briefly just before or during saccades, the rapid eye movement made to shift the point of gaze from one location to another. Mislocalizations in the dark have been reported to occur in the direction of the saccade and are roughly proportional to saccadic size (Cai et al. 1997; Dassonville et al. 1992, 1995; Honda 1989; Matin and Pearce 1965). However, during conditions of normal room lighting, briefly flashed peri-saccadic targets are mislocalized toward the endpoint of the saccade: stimuli flashed either left of right of the saccadic target are seen at the site of the target, implying a transient compression of visual space for briefly presented stimuli (Lappe et al. 2000; Morrone et al. 1997; Ross et al. 1997, 2001). The compression follows a precise time course, maximal at saccadic onset, stretching about 50 ms before and after. Compression has also been reported in total darkness, but it is less obvious and is related to a mislocalization of both the saccade target and the flashed object (Awater et al. 2000). Experiments with simulated saccades, using a moving mirror to duplicate the retinal events of a saccade without requiring that the subject actually make a saccade, clearly suggest that the apparent displacement of absolute position is mediated at least partially by an extraretinal signal or corollary discharge (Morrone et al. 1997; see also Ross et al. 2001).

The saccadic system is highly adaptive and can rapidly adjust to changes in the oculomotor musculature and plant that can be evoked by growth, injury (Kommerell et al. 1976), and fatigue (Barash et al. 1999). Although the adaptation occurs in the motor rather than perceptual system, the signal driving this adaptive process is the visual saccadic error, the distance between the fovea and the target at the end of the saccade (Wallman and Fuchs 1998). In the laboratory, this saccadic plasticity can be mimicked by a technique called short-term saccadic adaptation (McLaughlin 1967), which takes advantage of the inability of human subjects to detect small target displacements during saccades (Bridgeman et al. 1975). During adaptation, the saccade target steps in a stereotypical way at the beginning of the eye movement, toward or away from the fixation point. Although this target step is imperceptible to the subject, the oculomotor system interprets the saccadic error as being caused by an inappropriate saccade and adjusts the amplitude of the saccade appropriately. The adjustment is gradual, so that after a number of trials the eye ultimately lands on the final position of the target rather than its initial position.

Although saccadic adaptation is thought to affect primarily the motor system (Hopp and Fuchs 2002; Wallman and Fuchs 1998), two studies have shown that it also has perceptual consequences for targets presented well before saccadic onset. Moidell and Bedell (1988) reported small (about 0.5°) but consistent errors in perceptual localization during a fixation task after prolonged saccadic adaptation, suggesting a generalized distortion of visual space. More recently, Bahcall and Kowler (1999) measured the perceptual consequences of adaptation more directly by asking subjects to compare the apparent positions of pre- and postsaccadic probes during saccadic adaptation. The results show that subjects perceived the postsaccadic probes at the position where the eyes actually moved, even though this was quite far from the target that elicited the saccade. Bahcall and Kowler interpreted these results to imply that the "efference copy" signal used to stabilize perception during saccades is based on the intended saccade rather than the actual eye movement.

As mentioned previously, studies of peri-saccadic mislocalization show that the mislocalization is more complex than a simple shift, depending critically on retinal location: over a

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wide range of retinal positions, stimuli are localized toward a very strong attractor, the saccadic target. In this study, we planned to take advantage of this phenomenon to understand better the nature of the efference copy signal during saccadic adaptation, where the intended saccadic target is different from the actual target. To this end, we measured visual mislocalization of brief stimuli presented before, during, and after saccades, during conditions of saccadic adaptation. In particular we were interested in whether the focus of peri-saccadic compression would be determined by an intention-to-move signal or by the motor signal driving the actual saccade.

We report two major results. First that peri-saccadic focus of the compression (Ross et al. 1997) does not occur at the site of the initial saccadic target, but tended toward the actual landing site of the saccade. Second, and more surprisingly, we observed a large long-term perceptual distortion of space, lasting for hundreds of milliseconds. This distortion did not occur over the whole visual field but was limited to a local region of visual space around the saccade target, suggesting that saccadic adaptation induces a visuo-topic remapping of space. An abstract of these results has been presented elsewhere (Awater et al. 2001).

METHODS

Visual stimuli

Stimuli were displayed on a Barco color monitor with display area 36 × 25 cm, subtending 60 × 40° at the viewing distance of 37 cm. The display was surrounded by the dark brown frame of the monitor, lit to about 1 cd/m^2 by dim background illumination. Stimuli were generated at 250 Hz by a visual stimulus generator (Cambridge Research Systems VSG2) housed in a PC programmed in C. All stimuli were presented on a red background (Commission Internationale de l'Eclairage coordinates: $x = 0.595$; $y = 0.349$; luminance, 16 cd/m^2). The fixation spot and saccade target were black dots 1° in diameter. The test stimulus was a clearly visible vertical green bar, 2° wide and 40° high, presented for a single frame (4 ms) at an intensity nearly three times that of the red background. The contrast of the stimulus was always one log unit above detection throughout the entire course of the saccade (Diamond et al. 2000). For the data reported here, a black ruler was present on the screen 3° below the level of the fixation point. However, all conditions were also performed with the ruler presented 1000 ms after saccadic onset, giving substantially similar results as has been observed previously (Morrone et al. 1997; Ross et al. 1997).

Eye movement measurement

Eye movements were monitored by an infrared limbus eye tracker (HVS SP150) with 1,000-Hz temporal resolution. The horizontal resolution was 0.01°, and accuracy was 0.1° (manufacturer's specifications). In practice we observed an accuracy of about 0.2 ° over the range we studied. The infrared sensor was mounted below the right eye on transparent wraparound plastic goggles through which subjects viewed the display screen binocularly. The sensor was mounted close to the eye, so the subjects were unaware of its presence. The head of the subject was constrained by a chin-rest so that the eye was 37 cm from the screen. The PC sampled eye position at 1,000 Hz and stored the trace in digital form after suitable linearization. Before each session, both the gain and the linearity of the eye tracker were calibrated by asking subjects to make saccades to five fixed points arranged horizontally. Calibration was checked frequently during the recording sessions. Eye traces of subjects, together with target and stimulus presentation times, calibration, and subject responses, were stored in digital form for later off-line analysis.

Procedure

Observations were made in a dimly lit room, where the frame of the monitor was clearly visible. There were three types of trials.

UNADAPTED TRIALS. These were similar to those reported in a previous experiment (Morrone et al. 1997). Trials began with a dark fixation spot, which usually appeared 14° to the left of the center of the screen and stayed on thereafter. After a warning, the fixation spot disappeared and at the same time a target appeared (and thereafter stayed on) at center (0°), 14° right of center, or 20° right of center; subjects immediately saccaded to it, producing 14, 28, or 34° saccades. On each trial, a green bar was briefly presented (for 1 frame: 4 ms) either before, during, or after the saccade. Subjects were required to report the positions of bars with reference to the ruler by calling out a number to the experimenter. Subjects tended to report positions in integral numbers of degrees. If s/he did not see it, that trial was annulled (some conditions were particularly difficult to see, particularly bars in the far periphery, sometimes resulting in a paucity of data at a particular region). The arrangement of fixation spot, saccade target, ruler, and bar are shown in Fig. 1*C* (ignoring the white points at present). The experimenter checked the quality of each saccade and the computer's estimate of saccade onset and recorded the subject's reported position on the computer.

Average latencies for each subject were estimated after the first few trials, and this information was used to attempt to display the bar at a given time with respect to saccadic onset. However, actual delays were calculated off-line.

ADAPTED TRIALS. During saccadic adaptation, the target was caused to step as soon as the computer detected the onset of a saccade. When the horizontal eye position signal reached a predetermined threshold (relative to fixation), the target shifted abruptly to a new position, either closer to (gain decreasing) or further from (gain increasing) the initial target. After an initial training session, the saccade amplitude of the subject adapted gradually (usually within 20 trials) so the endpoint of the first saccade became progressively nearer to the new position of the target (Fig. 1*A*). We used three different intrasaccadic target steps: 14–20°, producing an increase in saccadic gain; 14–0°, producing a decrease in saccadic gain; 8–14°, producing an increase in saccadic gain (while not encroaching on the monitor border). As before, subjects were asked to report the position of the bar flashed before, during, or after the saccade, but the response was used only if the adaptation was within 5% of the actual target displacement.

Types of trials were blocked within a given session (gain increasing, gain decreasing, etc.), with 200–300 trials per session. The starting and finishing point of the trials was kept constant within each session to produce strong and stable adaptation, given the position specificity of adaptation (Alahyane and Pelisson 2003, 2004). Subjects usually perceived the target to be at the postsaccadic center of gaze. During the adaptation process, the subjects were sometimes aware of their own saccadic inaccuracy as evidenced by the necessity of the compensatory saccade. Fully adapted subjects were generally unaware of the adaptation process. The subjects never noticed the intrasaccadic shift. We assume that subjects did not use a deliberate strategy of gain change, because it did not occur immediately or all at once after a delay, but gradually over time (Fig. 1*B*). During conditions of adaptation, a trial was considered valid if the saccadic amplitude was within 5% of the actual displacement to the final target and if the target had been stepped to the final position within 10 ms of saccadic onset.

CONTROL TRIALS. We used two different types of control trials for some of the adaptation studies. In one, we occasionally (on 20% of trials) interposed trials in which the subjects were asked to judge the

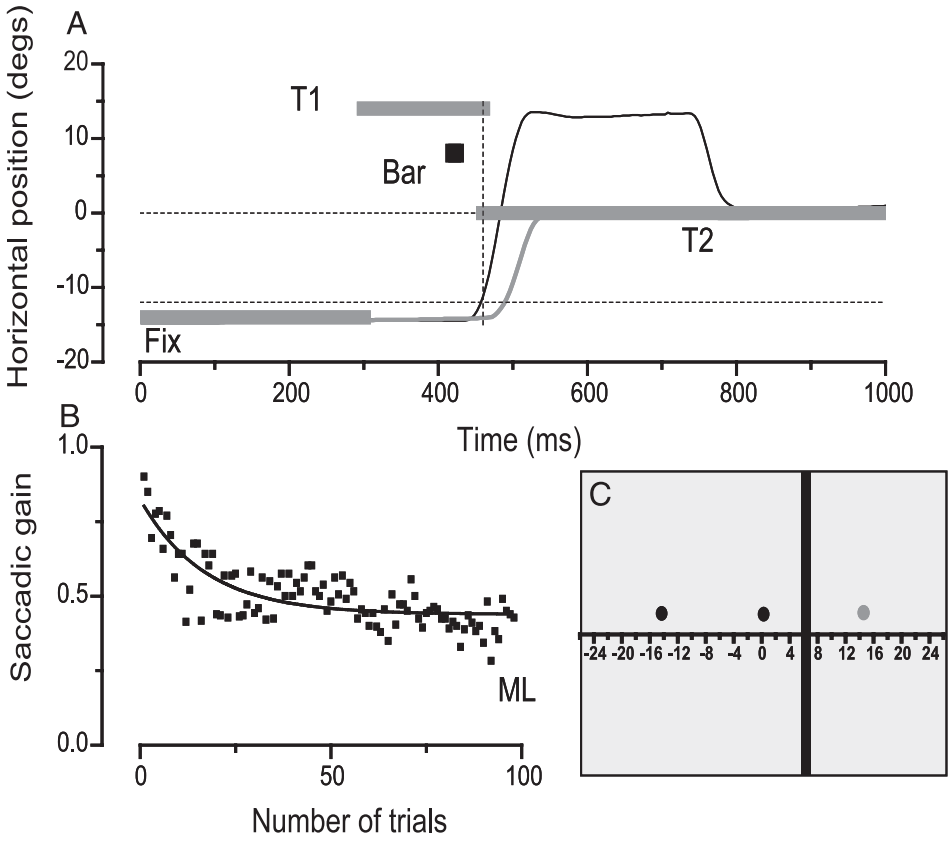

FIG. 1. *A*: time course of the various events that occurred on each trial in a particular adaptation condition (gain decreasing). Trial starts with the observer looking at the fixation point at left (position −14°). At an unpredictable moment, the fixation point disappeared and the target (T1: position +14° in this example) appeared at a particular position to the right, to which the observer made a saccade as rapidly as possible. During adaptation trials, the target was moved to T2 as soon as the computer had detected the onset of a saccade. Black trace shows a saccade early in the adaptation sequence, where the observer made 2 distinct saccades. Gray trace shows a later, perfectly adapted, saccade that went straight to the final destination. *B*: gain of the saccades (ratio of actual movement to distance to 1st target) in 1 experimental session, after training sessions. After a few trials, the saccade went straight to the final goal, one-half the initial distance (gain = 0.5). Curve passing through the data is an exponentially decaying fit with a constant of 19 trials. Even after adaptation, not all the trails met the strict criterion of being within 5% of the amplitude to T2. *C*: stimulus conditions for the experiments. Note that the fixation (−14°), saccadic targets (0 and 14°), and bar were never seen simultaneously, but followed the time course reported in *A*.

position of the bar without making any saccade at all (to see if the perceptual effects of saccadic adaptation were a general result of the adaptive process or required an actual saccade). Here the fixation spot remained on and the targets did not appear. The trial was only accepted if the subject continued fixation throughout the trial.

In another control, we interposed 15% catch trials in the adapted state experiments, in which the target never stepped on the saccade trigger but just disappeared. In these trials, the subjects were still asked to report the position of the bar (to see if the intrasaccadic target step caused any perceptual effect or if the subjects used the final target position as an aid to localize the flash.).

Subjects

Full data in the major conditions were collected from four subjects: two authors and two naïve to the goals of the experiment. However, all authors served as preliminary subjects for all conditions, and their results agreed with those of the more thoroughly studied subjects. We took particular care to randomize both the position of the bars and the time of their presentation within a given experimental condition, so subjects (both authors and naïve) were completely unaware of the conditions of a particular trial, given that people are very poor in localizing the time of presentation of a brief stimulus around the time of the saccade (Ross et al. 1997; Schlag and Schlag-Rey 2002). This minimizes the possibility of response stereotyping or other forms of bias in the data. The use of two naïve subjects for most major conditions further excludes this possibility.

Before collecting data on the adaptation conditions, we trained subjects for 1 or 2 days on the various adaptation regimens, until adaptation occurred within the first 20–40 trials. For each adaptation condition, 1000 trials were typically collected. Considering all the trials performed, including training trials, a small number of trials did not meet our stringent criteria of adaptation and were therefore eliminated. In many of the discarded trials, the subjects made compensatory second saccades. However, most of these errors occurred early in the adaptation process. Restricting the analysis to the session after training to achieve good adaptation, on average, 83% of all trials could be used for off-line analysis. Adding the remaining saccades did not change the overall pattern of results.

The experimental protocol was approved by the Consiglio Nazionale di Ricerca as being within its regulations for human experimentation under the Helsinki protocol.

RESULTS

Adaptation of saccadic gain

Before measuring visual mislocalizations around the time of saccades, we trained subjects in the saccadic adaptation paradigm of McLaughlin (1967). Subjects viewed a dark fixation spot 14° to the left of the center of the screen (see Fig. 1*C*). After a warning, a target appeared 14° right of center, to which subjects immediately saccaded. As soon as the saccade began, the target shifted to the new position (Fig. 1*A*). Initially, subjects made two separate saccades, first to the initial saccadic target followed by a corrective saccade to the new position (dark trace of Fig. 1*A*). Over the course of about 20 trials, the amplitude of the first saccade changed so that the endpoint of the saccade approximated the new position of the target, with the second saccade become smaller and of decreased latency (Fig. 1*A*). During this time, subjects ceased to perceive the intrasaccadic target shifts and usually perceived the target to be at the postsaccadic center of gaze.

Effect of saccadic adaptation on peri-saccadic spatial perception

This experiment was basically like that of Ross et al. (1997), except we also measured localization under conditions of gain

increasing and gain decreasing adaptation. Bright green bars were briefly flashed to one of four positions (−4, 4, 8, and 18°), and subjects were required to report where they seemed to appear (see Fig. 1 and METHODS for more details). In all conditions reported here, both the time of presentation relative to the target presentation and the actual spatial position were completely randomized, so subjects were unaware of the spatial and temporal condition of any given trial. The actual time of stimulus presentation relative to saccadic onset was determined during off-line analysis. During this analysis, we only accepted trials in which the saccade was within 5% of the final target (although data collection commenced before adaptation was complete).

Figure 2 shows average perceptual localization as a function of time relative to saccadic onset, for one of the four subjects used in this study (an author in this case). The three panels on the *left* show data for normal unadapted saccades of amplitude 14, 28, and 34°, starting from fixation at −14°. Within each panel, the mean and SE of the reported position of the bar is shown as a function of presentation time relative to the saccade; the horizontal lines of matched color show the actual position of the bars (−4°, red; 4°, blue; 8°, green; 18°, black). In this unadapted condition, the subject reported the bar near its veridical position when it is presented long before or long after the saccade. When the bar was presented in the interval immediately before or during the saccade, however, the subject made gross errors of mislocalization, reporting the bars close to the saccade target (T). The mislocalization errors were maximal near saccadic onset, and fell off steeply in a well-ordered fashion before and after, as described in detail elsewhere (Lappe et al. 2000; Morrone et al. 1997; Ross et al. 1997, 2001).

The two panels on the *right* show results for conditions of adaptation, either gain decrease of 50% (*top*) or gain increase of 21% (*bottom*), both with initial saccadic targets 28° to the right of fixation. Subjects had no difficulty in localizing the bars in the adapted conditions and reported that the task was subjectively very similar to that in the unadapted condition. Again there was very strong peri-saccadic mislocalization, leading to a transient compression of space. The focus of the compression was near the actual saccade goal rather than to the original saccade target. As for unadapted saccades, presenting the ruler 1 s after the stimulus had been displayed, rather than continuously, did not affect the results.

Furthermore, and quite unexpectedly, there was a systematic distortion of perceived position in some regions during the entire presaccadic fixation interval. In the gain decrease experiment, positions 4 and 8° (blue and green symbols) were severely mislocalized by as much as 8° in the direction of the gain decrease. This occurred very early with respect to saccadic onset, sometimes even before the appearance of the saccadic target (and the disappearance of the fixation point). Note that this distortion does not follow the same pattern as the peri-saccadic compression toward the saccadic target. In this case the shift is in the direction of the adaptation, although not uniform for all spatial positions.

For the gain increase experiment, the major early mislocalization occurred for position 18° (black symbols). Here the mislocalization was again strong, ≤6°, but in the other direction, again in the direction of the saccadic adaptation. In both cases the region of early mislocalization includes the region between the initial and stepped target positions. This result implies a form of trans-saccadic distortion limited to an area around the saccade target and its ultimate goal.

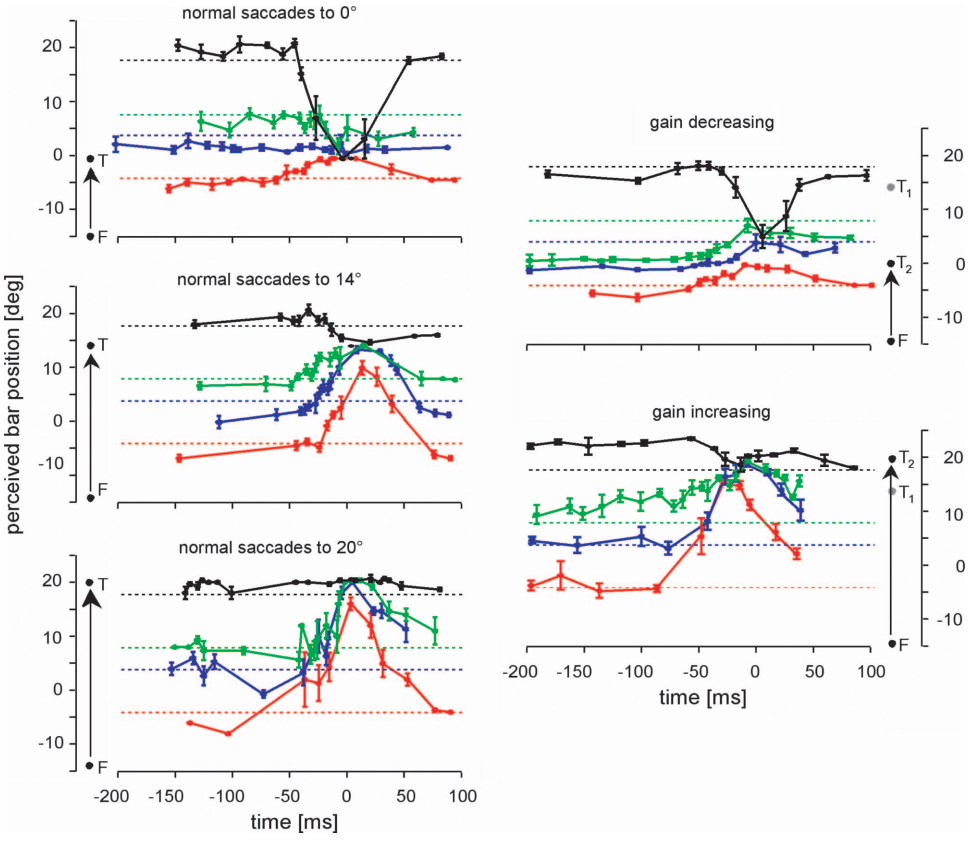

FIG. 2. Average perceived position of bars flashed at various times relative to saccadic onset (0 ms) in various positions under various conditions, for 1 subject (HA). Each point represents the average of 4–10 measurements, with error bars indicating SE. Each point is positioned at the mean time of bar appearance for the measurements. For each type of saccade, bars were flashed at 1 of 4 possible positions (randomly interspersed) indicated by different colors: −4° (red), 4° (blue), 8° (green), and 18° (black). Horizontal lines indicate the actual position, and symbols indicate average perceived position, together with SE. The 3 panels on the *left* show normal unadapted saccades of amplitude 14, 28, or 34°, shown by the vertical arrows at *left*. Panels on the *right* show results for gain decreasing and gain increasing saccades, shown by the arrows and targets at *right* (1st target T1 in gray). In unadapted saccades, the subjects grossly mislocalized all bars toward the saccadic target during the period near saccadic onset. In both the gain increasing and gain decreasing condition, they tended to be seen at the final landing point of the eye not the initial target that elicited the saccades. In both adapted conditions, there was also a strong mislocalization during the entire period before saccadic onset for bars flashed in the region between the 2 saccadic targets. Mislocalization was in the direction of the adaptation.

To rule out the possibility that the compression to the final target was caused by the physical presence of that target, we performed another control experiment using catch trials. Every now and again (unpredictably, but on average 1 trial in 5) we presented well-adapted subjects with trials in which the saccade target disappeared but never reappeared. The subjects made the adapted saccades as expected even though there was no intrasaccadic target step. In these conditions, as before, compression was toward the final landing point of the eye, even though there was no actual target there (Fig. 3). The early mislocalization in the region between saccadic target and landing point also occurred.

We studied peri-saccadic localization (for trials that occur in the 20-ms interval before saccadic onset) over a finer spatial scale. The results of four subjects (2 authors and 2 naïve) are shown in Fig. 4 as a function of real spatial position of the bars. The adapted (filled symbols) results are shown together with unadapted saccades of the same actual amplitude (open symbols). The results of all subjects are quite similar in both conditions. Compression tended to be around the final landing point of the eye, not the intended eye movement. That is to say, irrespective of the actual position of where the bar was presented, it tended to be seen at the second saccadic target, 0° in the case of the gain-decreased saccades and 20° in the case of the gain-increased saccades. There were some individual differences in this general trend, particularly for subject MCM who showed less compression for the more peripheral targets with the gain decreased saccades.

To describe better the effects of adaptation on saccadic compression, we calculated the "focus of the compression" for all four subjects. The focus was calculated from the data of Fig. 4, by regressing the errors in localization against real position

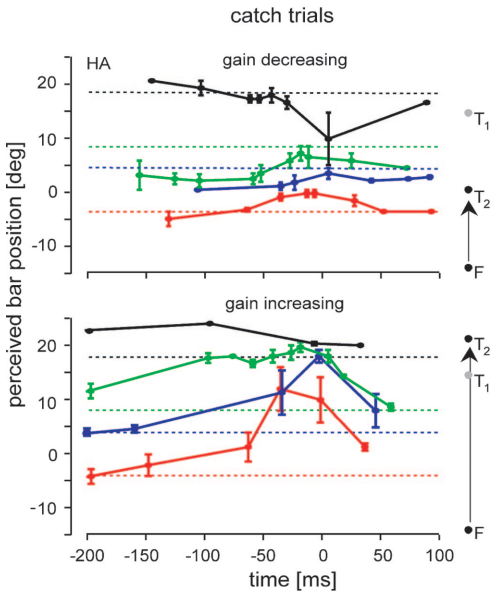

FIG. 3. "Catch trials": after an initial period of adaptation, on every 3rd to 7th trial (1/5 on average), the 1st target T1 disappeared after the saccade but the 2nd target T2 did not appear in its new position on that particular trial. Each data point is the average of 2–4 measurements, with error bars representing SE. On the other trials (not reported here), the normal adaptation sequence (with target displacement) continued to maintain adaptation. Although there are necessarily far fewer trials in this condition, results basically confirm those of Fig. 2, showing that it is not the presence of the 2nd target that causes mislocalization.

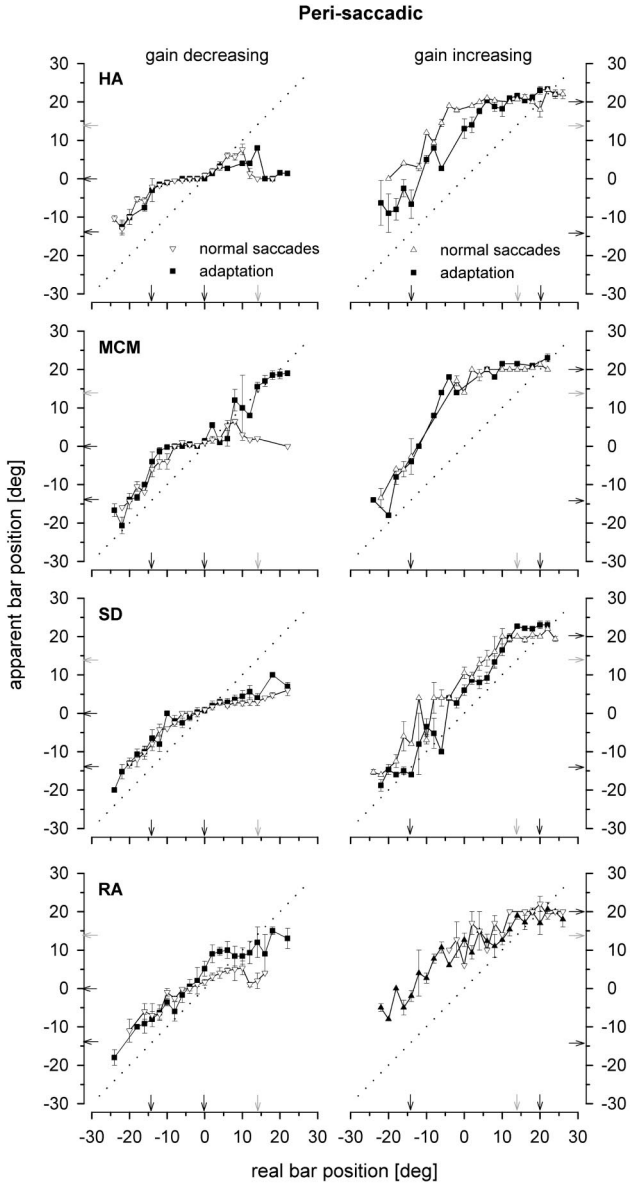

FIG. 4. Mislocalization during the interval just before saccadic onset (–20 to 5 ms), as a function of space, for gain decreasing (*left*) and gain increasing (*right*) saccades. For comparison, unadapted saccades (matched to actual movement) are shown as open triangles. Each point represents the average of 4–10 measurements, with error bars indicating SE. Dotted lines indicate expected results for veridical perception, and symbols indicate average perceived position (average of 4–10 trails), together with error bars. Arrows indicate fixation point (lowest arrow in each panel), the 1st saccadic target (pale gray), and the 2nd saccadic target. In all cases, there were gross distortions in perceived position, with a strong compression around the saccadic target. In general, the compression was to the final landing point of the eye (dark arrows), not to the initial target (light arrows) that elicited the saccades. For the gain decreasing saccades for subject MCM, the compression was limited to the 14° of space between fixation and landing point.

and estimating the zero intercept. These estimates are shown in Fig. 5 for all four subjects. The abscissa indicates the five relevant conditions: short, medium, and long unadapted saccades, together with gain decreasing and gain increasing adapted saccades, where the first target corresponded to the medium saccade and the final target to the short or long saccade, respectively. For the normal saccades, the compression was usually very close to the saccadic goal: 0, 14, or 20°.

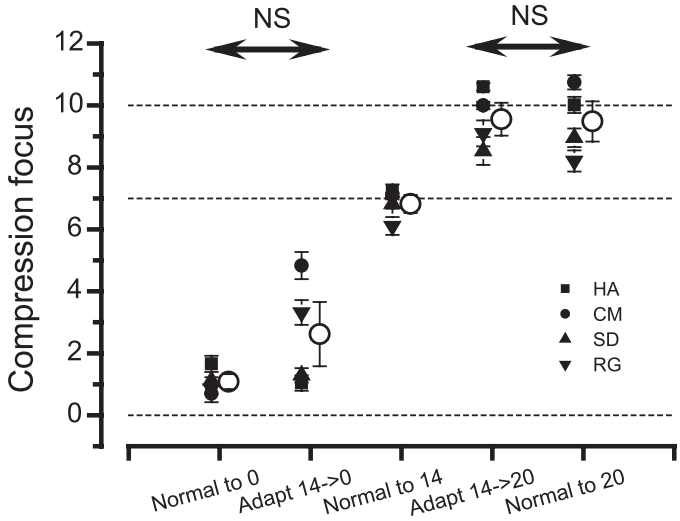

FIG. 5. Focus of compression for the 4 subjects for whom complete data were taken. Focus was calculated from the data of Fig. 4, regressing the errors (deviations from real position) against real position and estimating the intercept, weighting each point by its SE. If the linear regression for all spatial positions accounted for <80% of the variance, the range of the regression was limited to points to the right of fixation. Time window was between −20 and +5 ms relative to saccade onset. Filled data points show foci for individual observers, with error bars indicating SE of the intercept estimation. Open data points are average results, with error bars indicating SE between subjects. A 1-way ANOVA revealed a highly significant main effect ($P < 0.001$, $F = 66$, $df = 4$). Pair-wise multiple comparisons revealed significant differences between all possible pairs except those indicated by the arrow labeled "NS." Average compression foci for both adaptation conditions were significantly different from those to the primary saccade target (14°): $P < 0.001$ for gain-decreasing and $P = 0.02$ for gain-increasing. HA and CM were authors; SD and RG were naïve.

With adaptation, the compression was more toward the final goal than the initial target. There were some variation between subjects, but the average trend (large open circles) was clearly toward the saccadic endpoint.

A one-way ANOVA revealed a highly significant effect of saccade type ($P < 0.001$, $F = 66$, $df = 4$). Pairwise multiple comparisons of the group data revealed significant differences between all possible pairs *except* between normal saccades to 0 and gain decreasing saccades with endpoint 0° ($P = 0.5$) and between normal saccades to 20° and gain increasing saccades with endpoint 20° ($P = 1$). The average compression foci for both adaptation conditions were significantly different from those to the primary saccade target corresponding to the intention to move (14°), $P < 0.001$ for gain decreasing and $P = 0.02$ for gain increasing. This confirms the suggestion that the focus of saccadic compression during adaptation tends to be the final landing point of the eye rather than the initial target that elicited the eye-movement.

A possible problem with the gain increased saccades was the effect of the screen border. To minimize this factor, we studied an adaptation sequence in which the initial target point was closer to the center of the screen (8° right of center), so the second point remained quite far from the edge (16° from the edge). Here also, compression moved to the actual endpoint of the saccades whether they were adapted or unadapted (Fig. 6).

Extent of trans-saccadic perceptual distortion

As noted in Fig. 2, stimuli presented to some spatial positions well before the saccade were also mislocalized, even when presented several hundred milliseconds before saccadic onset. To examine this phenomenon further and to determine its spatial extent, we presented bars well before a saccade (>150 ms) to all spatial positions. Again the spatial positions and presentation times were randomized from trial to trial to minimize response stereotyping.

Figure 7 shows the results for same four subjects as in Fig. 4: two authors (*top*) and two naïve subjects unaware of the goal of the experiment (*bottom*). The data on the *left* show results for adapted saccades, both gain increased (○) and gain decreased (■), with the dotted line showing veridical response. The deviations from this line (errors in mislocalization) are not uniform over space but extend roughly from the fixation point toward the saccade goal. They are strongest in the region that lies between the saccade target and its ultimate landing point. There was also distortion in the region immediately adjacent to this and some variation from subject to subject, but all subjects showed a robust shift in the direction of the adaptation and only over a limited area centered around the region between saccadic targets.

For unadapted saccades, localization of objects flashed well before saccadic onset showed only a small deviation from the veridical, usually in the same direction for the short and long saccades (Fig. 7, *right*). A two-way ANOVA was performed for each subject, revealing significant differences ($P < 0.05$ in all cases) between gain increasing and gain decreasing adapted conditions, but no significant differences for localization during normal saccades.

Given that the distortions during saccadic adaptation occur for very large durations before saccade onset, we asked if the saccade was necessary at all: perhaps space becomes distorted during adaptation, even for normal viewing. To test this we interposed trials in which the fixation point never disappeared, and instructed subjects not to make a saccade in these conditions. For these trials, shown in Fig. 8, the pattern of results was quite different from for the trans-saccadic localization. There were some small deviations from veridical (especially for subject HA), but these were much less than with the saccade, and the shift was not specific for the direction of the adaptation.

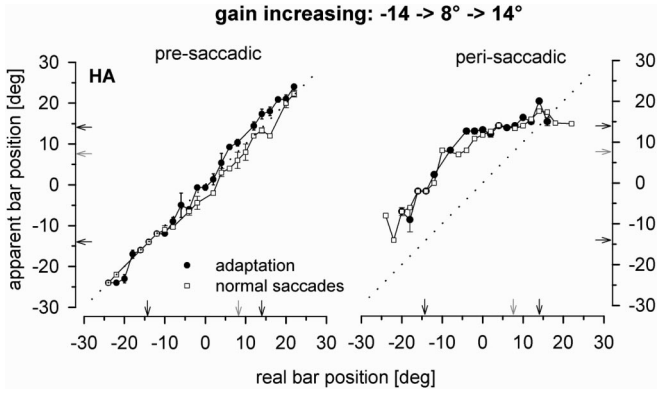

FIG. 6. Gain increasing saccades of smaller amplitude (22 → 28°), finishing well away (16°) from the edge of the screen, to exclude the problem of visual interference of the edge. Fixation was at −14°, T1 at +8°, and T2 at +14°. Results are substantially the same as those observed with the larger saccades, both for presaccadic presentations (Fig. 7) and peri-saccadic presentations (Fig. 4). Other details are given in the captions to those figures.

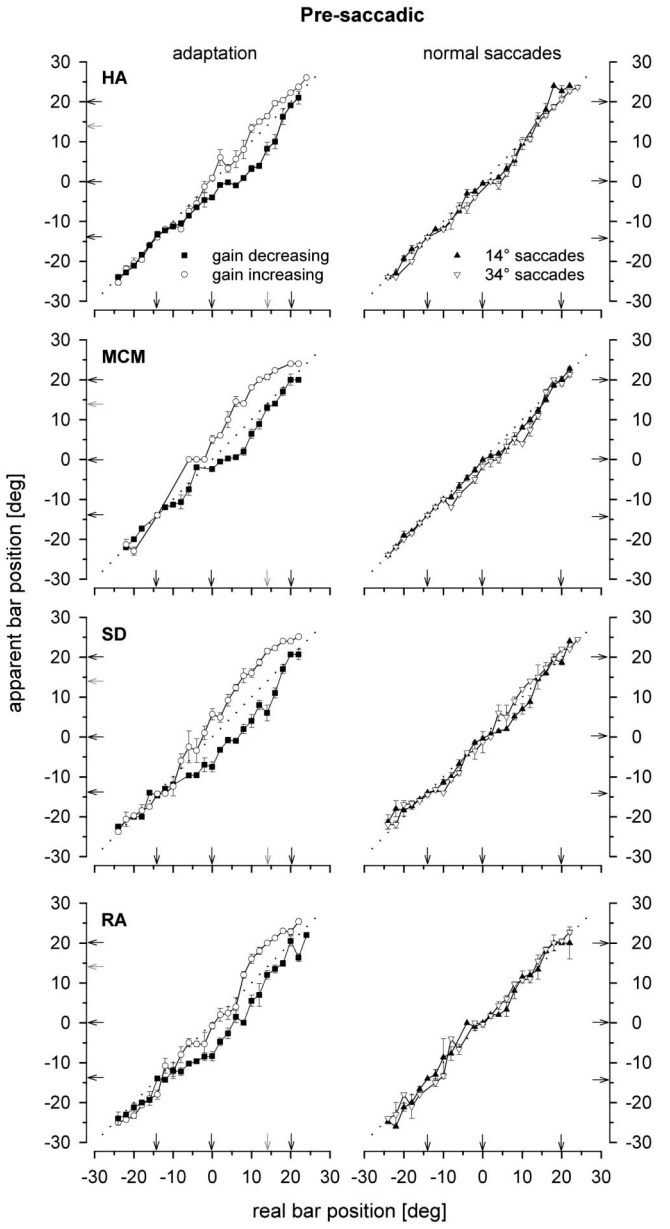

FIG. 7. Perceived position of bars flashed well before saccadic onset (–500 to −150 ms), plotted as a function of real position of the bar. Bars were presented at random to all positions, with a spatial grain of 2°. Each point represents the average of 4–10 measurements, with error bars indicating SE. Panels at *left* show results for adapted saccades (■, gain decreasing; ○, gain increasing), and those at *right* show results for normal saccades of the same actual amplitude (▲, 14°; △, 34°). Arrows on the axes indicate the key saccadic targets. Black arrow at –14° is the fixation point, and the gray arrow at +14° is the initial saccadic target. Black arrows on either side of this are final targets for gain decreasing and increasing conditions. Over a limited region, corresponding roughly to the area between the 2 saccadic targets, space was grossly distorted during adaptation in the direction of the adaptation. There were also some mislocalizations during normal saccades, but they were not so systematic, nor of the same magnitude.

DISCUSSION

These experiments report two main effects of postsaccadic spatial localization during saccadic adaptation. First, targets briefly presented around the time of saccades show the type of compressive mislocalization pattern previously reported for normal saccades (Ross et al. 1997). The focus of the compression tends to be closer to the endpoint of the actual movement rather than the target that evoked the saccade, and indeed the entire mislocation curves of adapted saccades are very similar to those obtained with unadapted saccades of the same amplitude. Second, during periods of adaptation, stimuli presented well before the saccade to certain regions of space were mislocalized.

That the compression focus should follow the actual rather than the planned saccade is not entirely expected from previous work on adaptation. For example, during saccadic adaptation, the attentional focus of human subjects, measured by contrast sensitivity, remains at the spatial location of the original target, even though the actual saccade is made to a different target (Ditterich et al. 2000). In those experiments, subjects had to report the orientation of an object but not its position. Our experiments did not examine stimulus detectability or other indices of attention, but localization of a high contrast and clearly visible bar. It is interesting that, although the attentional focus remains with the initial saccadic target, saccadic mislocalization occurs toward the endpoint of the actual movement.

Compression did not depend on postsaccadic visual information from the target itself. We performed controls where the subject was well adapted, but rather than stepping to a new position, the target disappeared completely. The results with these catch trials were essentially the same as when the target was moved, showing that the actual presence of the target was not necessary as a visual or attentive reference in these experiments. However, in the absence of a postsaccadic target, memory information about the usual postsaccadic target position in the adaptation trials might have been used together with physical visual references provided by the ruler and the monitor edges (Lappe et al. 2000). The role of visual references in peri-saccadic mislocalization has been debated over several years. Although it is clear that visual references have a strong effect on mislocalization (e.g., Honda 1999) and, in particular, on compression (Lappe et al. 2000), mislocalization does occur in total darkness (e.g., Cai et al. 1997; Matin and Pearce 1965). Recently it has been shown that visual compression also occurs in darkness, provided that the mislocalization of the saccadic target itself is considered (Awater et al. 2000). These results

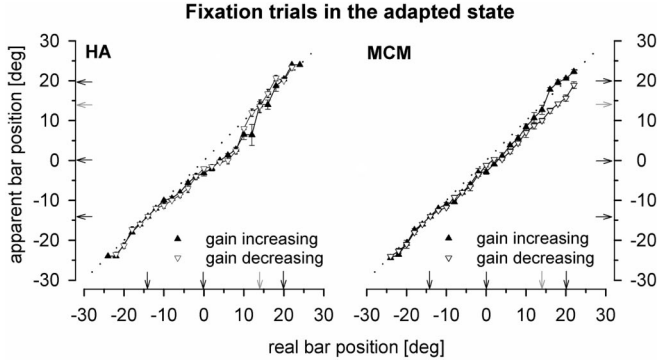

FIG. 8. Measurements of apparent position during fixation while subjects were adapted (decreasing and increasing gain). On 20% of trials (on average), the fixation point did not extinguish, and on these trials, the subject did not make a saccade: all else was the same as before. Each point represents the average of 3–6 measurements, with error bars indicating SE. Here there were some mislocalizations (especially for HA), but lower magnitude than when an actual saccade was made. Importantly, errors were in the same direction for gain decreasing and gain increasing saccades.

show that compression does not result entirely from visual references, but may also involve an extraretinal signal.

There are two general possibilities of how an extraretinal signal could act in trans-saccadic spatial localization. An extraretinal signal could be used to construct an impression of position of a visual target in space (Matin and Pearce 1965), but this role is only clearly applicable when targets are in darkness. When other visual references are available, the role of the extraretinal signal becomes more complex (cf. Dassonville et al. 1995; Deubel et al. 1998; Honda 1999). For example, an extraretinal signal could affect mechanisms that determine relative visual position (Lappe et al. 2000). The reference object theory of trans-saccadic spatial localization (Deubel et al. 1998) assumes that the position of objects before the saccade is encoded relative to reference objects, the most obvious reference being the saccade target. After the saccade, the position of the object has to reconstructed from the encoded relative position, the extraretinal signal, and the reference position of the saccade target. Lappe et al. (2000) proposed that the compression originates in the encoded relative distance between flash and target.

How would the data of our experiments fit with the reference object theory? One would have to assume that the flash position is first encoded—and compressed—toward the initial visual cue at T1, and after the saccade reconstructed with respect to the postsaccadic target position at T2, using a combination of visual and extraretinal references on T2's position itself. Thus the center of compression should eventually lie at T2. However, the theory essentially predicts that this is the result of two separate processes: peri-saccadic compression of relative distances in the scene encoded at the time of the flash plus a transformation from T1 to T2 because of the saccade adaptation. The long-lasting space distortion that we observed long before the saccade can help to distinguish these two stages because it clearly relates only to the transformation induced by saccade adaptation. The theory predicts that peri-saccadic effects can be seen in isolation when the adaptation effects are subtracted. For instance, for the data in Figs. 2 and 3, this would mean to shift each curve such that the data points long before the saccade are aligned with the true positions (dotted lines). Indeed, the peri-saccadic data points of the blue, green, and black curves in Figs. 2 and 3 would fall close to position T1, consistent with the theory. The red curves, however, do not follow the prediction.

The functional role of saccadic compression is still poorly understood, although it has been confirmed in many laboratories over several years. However, whatever its actual role, it is a useful tool to study peri-saccadic mislocalizations, because they can be characterized by a single attractor point. The fact that peri-saccadic mislocalizations during adaptation follow closely the pattern generated by an unadapted saccade of same actual size can be interpreted in one of two ways: either there exists an efference copy signal of the same size as the actual saccade or the effect results entirely from the postpositioning of the eye. The second possibility would suggest that visual stimuli briefly flashed around the time of the saccade are always seen at the final landing point, irrespective of whether the saccade was planned to that point or whether the landing point was different from that expected, due to adaptation. Perhaps objects presented around the time of saccades are not localized well by the visual system, because of shown suppression of the magno-cellular system (Burr et al. 1994; Ross et al. 1996). Indeed, the strength of compression correlates with the strength of suppression (Michels and Lappe 2004). The default localization of all stimuli flashed around the time of the saccade is the fovea. In any event, this explanation also requires an extraretinal corollary discharge suppression signal at the time of the saccade (Diamond et al. 2000). A somewhat similar explanation was proposed by Niemeier et al. (2003), who showed that saccadic suppression of displacement occurred most dramatically at the saccade goal and correlated with the unreliability of individual subjects' saccades. They interpreted these data to suggest that the brain uses an optimal inference solution one property of which is to compress stimuli toward the center of gaze.

The alternate explanation is that the mislocation is driven by an efference copy signal matched to the actual not intended saccadic amplitude. It is not obvious where this extraretinal signal may come from, particularly in the adapted condition. Saccadic adaptation, although driven by visual error, occurs on the motor side, involving the fastigial nucleus (Robinson and Fuchs 2001) and vermis (Barash et al. 1999). PET studies in humans implicate the cerebellum (Desmurget et al. 1998). Neurons in oculomotor supranuclear areas such as the superior colliculus do not show evidence of adaptation (Frens and Van Opstal 1997), suggesting that the colliculus and the cortical areas that project to it specify target location in unadapted visual coordinates and that the motor program for the adapted saccade is determined by downstream centers. However, the peri-saccadic localization errors seemed to be driven by the final landing point in the adapted condition, suggesting that if an efference copy signal is driving this compression, the signal must arise after cerebellar modification of the visually determined saccade goal. This signal would have to ascend to the visual areas of the cerebral cortex. Recently, Sommer and Wurtz (2002) showed that a lesion in the medial dorsal nucleus of the thalamus, which relays the superior colliculus saccadic signal to the frontal eye field, partially affects the monkey's ability to perform double-step saccades, a task for which efference copy is necessary. This pathway, which would be expected to be unaffected by saccadic adaptation, could not supply the entire efference copy signal in the adapted state.

Besides the data on peri-saccadic localization, showing a dynamic remapping at the time of the saccade, we also showed a long-lasting distortion of spatial localization of targets presented long before the saccade. This result bears on issues of spatial memory and trans-saccadic integration. This result somewhat resembles that of Bahcall and Kowler (1999), who showed spatial mislocalization of objects presented in darkness near the locus of the saccade target. They limited their investigation to perceptual localization of the first saccadic goal, and concluded that the efference copy that compensated for the physical motion of the image across the retina was driven by the "intention to move" signal rather than the actual eye movement. The two studies agree in showing perceptual mislocalizations of stimuli displayed well before saccade onset in the direction of the adaptation. We further showed that the mislocalization occurred over a limited area of the visual field, the area near the saccade goal and the final saccade endpoint. For the rest of the visual field, postsaccadic estimation of the spatial location of a presaccadic stimulus is accurate except for times very near saccadic onset.

Bahcall and Kowler explained their result in terms of an inappropriate efference copy, set by the intention to move signal rather than the actual motion. While this explanation could explain our results near the saccadic target, it cannot explain the whole pattern of results shown in Fig. 7: a single inappropriate efference copy signal would shift the entire curves leftward or rightward by a constant amount, proportional to the mismatch. However, our results clearly show that the distortion of space is limited to a region including the first and second saccadic targets. Bars displayed outside this region were localized veridically. For this veridical region, the mechanism that compensates for saccades must be an accurate efference copy of the actual, not the intended, saccade, or some other signal. There must be a special mechanism that compensates for the part of space around the saccadic targets. This part of space, which is distorted by the motor system, seems to be also distorted by the perceptual system for a long interval between the appearance of the target and the performance of the saccade.

The presaccadic long-lived shift requires that the subject actually make a saccade and report the location of the flashed object after the saccade. Our subjects did not show such a shift when, even though they were adapted, they reported the location of a flashed object without performing a saccade. Moidell and Bedell (1988) reported a small shift (0.5°) in a similar saccadic adaptation experiment without actual saccades. However, this shift is of much lower magnitude than that reported here, below the resolution of our experimental technique.

One exciting possibility is that the presaccadic distortion that we observe here constitutes, or at least contributes to, the actual mechanism of saccadic adaptation. However, this tempting idea seems unlikely for many reasons. First, a great deal of evidence suggests that saccadic adaptation occurs in the motor system rather than the visual system (e.g., Wallman and Fuchs 1998). Second, although saccadic adaptation does show spatial selectivity (Deubel 1991; Frens and van Opstal 1994; Noto et al. 1999), the reported spatial selectivity of the adaptation field is not co-extensive with the area of long-lived perceptual shift. In gain-decreasing adaptation, the area beyond the target position is strongly adapted, yet we found little or no long-lived perceptual shift in this region. Third, we found this mislocalization only for briefly presented targets. We have no information of whether targets continuously displayed for longer periods would be mislocalized. Therefore although we cannot exclude completely this hypothesis, it seems likely that the mechanisms underlying the parametric adaptation field and the long-lived perceptual shift are not the same.

The results for presaccadic localization may also be considered in terms of the previously mentioned "*reference object theory*" (Deubel 2003; Deubel et al. 1998), which assumes that pre- and postsaccadic "snapshots" are linked to a limited region around the saccadic target, which the visual system assumes to be stable. In our experiment, the saccadic target stepped imperceptibly during the saccade so the postsaccadic fixation should be linked to a different portion of the presaccadic fixation, causing a local distortion. This distortion was limited to a region of about 20° around the saccadic targets. With a quite different experimental paradigm, Deubel (2003) showed distortion limited to about 3° of space; however, in his experiment, the saccades were only 6°, compared with the 28–34° saccades used here, suggesting that the extent of the region depends on saccadic amplitude.

These data reinforce the concept that human spatial memory, introspectively robust, is in fact rather fragile. It depends on a number of independent metrics that are ordinarily in register, but which can be dissociated. When eye movements and the visual scene are out of joint, the brain struggles as best it can, using both corollary discharge and memory. On the other hand, these data also show a high potential for plasticity in perception, limited to the relevant region of visual space.

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