

Influence of saccadic adaptation on spatial localization: Comparison of verbal and pointing reports

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Under conditions of short-term saccadic adaptation, stimuli presented long before saccadic onset are perceptually mislocalized in space. Here we study whether saccadic adaptation can also affect localization of objects by pointing. We measured localization performance during fixation and after normal saccades and adapted saccades, for a bar presented well before a saccadic eye movement, for both pointing and verbal localization, under open-loop conditions generated by a transient dark period about 300 ms after the presentation of the bar. During fixation and normal saccade, localization performance for verbal report was veridical, while for pointing there was an overestimation of the target eccentricity respect to gaze, in agreement with the idea of separate representations of space for action and perception. During saccadic adaptation, there was a significant shift of both pointing and verbal report localization in the direction of adaptation with similar spatial selectivity for both tasks. These results indicate that saccadic adaptation induces a similar re-calibration of the action map as well as of the perceptual map, suggesting a common site of operation in the transformation from eye-centered to gaze-centered coordinates.

Keywords: saccades, adaptation, pointing, localization

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Introduction

Information about eye-position is essential for encoding spatial positions of visual stimuli in head-, body- or world-centered coordinates (for review see Pouget, Deneve, & Duhamel, 2002) and it is known that the eye-position signal may alter the ability to localize a visual stimulus in the external world both during fixation (Enright, 1995; Lewald & Ehrenstein, 2000) and during eye movements (Brenner, Smeets, & van den Berg, 2001; Ross, Morrone, & Burr, 1997). During fixation, some studies have reported a compression of the perceived positions in the direction of the fovea (Mateeff & Gourevich, 1983; van der Heijden, van der Geest, de Leeuw, Krikke, & Musseler, 1999), while others reported an overestimation of stimulus eccentricity (as referred to gaze direction) (Enright, 1995; Lewald & Ehrenstein, 2000) and the two different patterns of result may depend on the visual cues present. Also, localization by pointing, in the absence of visual information, tends to produce an overestimation of the eccentricity effect (Bock, 1986; Bock & Eckmiller, 1986; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Medendorp, Van Asselt, & Gielen, 1999). These errors in localization for the different eccentricities of the eye have often been thought to reflect an inaccuracy of the processes integrating retinal information and eye-position to transform gaze-centered coordinates into higher-level allocentric coordinates.

A direct comparison between localizing a stimulus by blind pointing and by verbal report yields a different pattern of localization ability and errors in some experimental conditions, reinforcing the hypothesis of separate processing of visual information for perception and action (for review see Goodale & Milner, 1992; Goodale & Westwood, 2004). In particular, Burr, Morrone, and Ross (2001a) and Morrone, Ma-Wyatt, and Ross (2005) showed that blind pointing to perisaccadically flashed stimuli is not affected by the visual space compression that was observed for the same stimuli with verbal report. These results imply that localization of visual stimuli can access different maps of visual space: a “perceptual” map for normal lighting conditions that is subject to compressive space distortions and an “action” map that can guide pointing localization in the absence of visual references. The action map would be more stable and less subject to compressive distortion. However, the motor map can be highly adaptive and can be modified by experience. Here we address the question of whether alteration of an oculomotor map during saccadic adaptation may lead to a similar dissociation between perceptual and action representation of space. If the alterations are similar we can hypothesize a common mechanism that may serve to recalibrate both maps.

Saccadic adaptation is a mechanism used by the oculomotor system to maintain saccade accuracy in the face of variability in muscle strength and other factors. Without saccadic adaptation patients with eye muscle

weakness or neural damage would produce persistently dysmetric saccades, as has been shown with humans (Abel, Schmidt, Dell’Osso, & Daroff, 1978; Kommerell, Olivier, & Theopold, 1976) and primates with lesioned oculomotor muscles (Optican & Robinson, 1980). A short-term form of saccadic adaptation can be induced behaviorally by shifting the saccadic target to a new position (backwards or forwards) after the subject has started to execute an eye-movement towards the initial target position. Although the target jump is not consciously perceived by the subject (Bridgeman, Hendry, & Stark, 1975), the oculomotor system senses the initial saccade inaccuracy and initiates a corrective saccade to position the eye on the actual position of the target. Repeating the procedure over several trials leads to a gradual change of the amplitude of the initial saccade to achieve the final position of the target with a single saccade (McLaughlin, 1967; Straube & Deubel, 1995; Watanabe, Ogino, Nakamura, & Koizuka, 2003). Retinal error (defined as the postsaccadic difference between fovea and target position) is supposed to be the signal that guides saccadic adaptation (Seeberger, Noto, & Robinson, 2002; Shafer, Noto, & Fuchs, 2000; Wallman & Fuchs, 1998). However, adaptation occurs only over a selective range of directions and amplitudes of the error (target jump), both in monkeys (Straube, Fuchs, Usher, & Robinson, 1997) and in humans (Frens & van Opstal, 1994). Interestingly, the amount of adaptation transfer from one target step to another is not uniform across all possible amplitudes and the more the step amplitude differs from the adapted one, the smaller the transfer is (“adaptation field”: Frens & van Opstal, 1997).

Saccadic adaptation induces mislocalization of visual targets (Moidell & Bedell, 1988). Bahcall and Kowler (1999) showed that, during saccadic adaptation, the first saccadic target is mislocalized in the direction of adaptation, when it is briefly flashed about 200 ms before saccadic onset. They interpreted the shift of perceived position as resulting from the process of recalibrating perceptual space maps and associated the error to an erroneous “intention-to-move” signal, different from the actual eye movement, not adapted during adaptation. Awater, Burr, Lappe, Morrone, and Goldberg (2005) replicated the data of Bahcall and Kowler (1999) in very different experimental conditions (in the light and in presence of stable visual references that could in principle annul the localization error) and, in agreement with the previous study, showed that the error is present only if the saccade is performed and the subject is adapted. They also measured the time course of the mislocalization and its spatial specificity: they noticed that the shift in the direction of adaptation is not peri- or post-saccadic, but it occurs only for targets presented very early with respect to the saccadic onset; and that the shift is not constant across space, but it is restricted to a narrow range around the saccadic target. Awater et al. (2005) concluded that the mislocalization may reflect a plastic, albeit transient,

alteration of the perceptual space induced by the motor adaptation.

Previous studies have also shown that pointing to a visual target is altered by saccadic adaptation. Bekkering, Adam, van den Aarsen, Kingma, and Whiting (1995) found a significant transfer of saccadic gain-reducing adaptation (an adaptation level of 50% of the second target jump for eye-movements and 41% for hand-movements) to pointing movements when subjects had to make both a saccadic eye movement and a hand pointing movement to the target (no visual feedback was available from the hand and they manipulated the eye error-signal and not the hand error-signal). The transfer found by Kröller, De Graaf, Prablanc, and Pélisson (1999) in similar experimental conditions was much smaller, though significant (close to 15%), and limited to gaze-shortening adaptation. There is evidence also of a transfer of saccadic adaptation to other visuomotor behaviors. In monkeys Phillips, Fuchs, Ling, Iwamoto, and Votaw (1997) described the existence of a significant gain transfer to the eye- and head-movement components of head-unrestrained gaze shifts after a gain-reducing saccadic adaptation obtained in a head-restrained condition. However, Kröller, Pélisson, and Prablanc (1996), measuring head-pointing movements in human subjects before and after saccadic adaptation, found no transfer of adaptation from one motor output (saccades) to the other (head movements).

Here we study the possible dissociation between perceptual and action maps, first in a fixation task at different gaze eccentricities and then under conditions of saccadic adaptation. The major result indicates that while the dissociation is clear during fixation, the saccadic adaptation influences to a similar extent both the perceptual and the action representation of external space.

Materials and methods

Subjects

Two of the authors (AB and MCM) and a naive subject (ES) completed each of the conditions described below. Visual acuity was normal or corrected to normal in all subjects and all but one (AB is a red-green dichromat) had normal color vision. All were right handed.

Apparatus

Stimuli were generated at 200 Hz by a visual stimulus generator (Cambridge Research System Vsg 2/4F) driven by Matlab programs. They were displayed on a Barco Calibrator monitor, which subtended $35^\circ \times 25^\circ$ at the viewing distance of 60 cm. The fixation spot and the saccadic targets were black dots 0.5° in diameter. They

were both positioned 11.5° from the top of the screen, with the fixation spot 8° left of center of the screen and saccadic target 1° , 4° or 8° right of center, for the different experimental conditions (see [Procedure](#)). The stimulus to be localized was a clearly visible blue vertical bar (Commission Internationale de l'Eclairage (CIE) coordinates: $x = 0.144$; $y = 0.07$ mean luminance: 7 cd / m^{-2}), 0.4° wide and 25° high, which was randomly displayed for a single frame duration (5 ms) at one of 29 possible positions (the range was 14° left of screen centre to 14° right of screen centre; the horizontal distance between contiguous positions was 1°). All stimuli were displayed on a red background (Commission Internationale de l'Eclairage (CIE) coordinates: $x = 0.621$; $y = .344$; mean luminance: 13.5 cd / m^{-2}).

Eye-movement measurements

Subjects sat in a room facing the monitor, with all other machinery (pc, eye-tracker monitor and controller) in a separate room. The head of the observer was constrained by a neck-rest (mounted on the back of a comfortable chair) to minimize head movements and to keep the distance between the eye and the monitor constant at 57 cm. Eye-movements were recorded with an infrared limbus eye-tracker (HVS SP150). The horizontal resolution was 0.01 degree and accuracy was 0.1 degree. Calibration was performed at the beginning of the recorded sessions and checked very frequently. The infrared sensor was mounted below the left eye on Cambridge Research Systems ferroelectric liquid crystal shutter goggles through which the subjects could see the monitor binocularly.

Eye-position measurements for one subject (AB) were initially recorded by means of an Applied Science Laboratories eye-camera (model 504 EYEPOS at 240 Hz). We decided to move to the limbus system because the ASL has a constant delay of approximately 8 milliseconds in recording the saccade. This induced a delay in the trigger of the stepping of the saccadic target making adaptation less stable (see [Procedure](#)). The pattern of results obtained with the ASL eye-camera (which has a higher spatial resolution and, consequently, a better gain definition) was not significantly different from that obtained with the limbus machine.

Procedure

At the beginning of each trial, subjects sat in front of the monitor with both hands resting on their lap, one upon the other (they were explicitly asked to do so). Each trial started with the goggle-shutter opening and the display changing from the black frame to the red frame background. On separate sessions in the same or consecutive days each subject performed three different experiments (fixation, normal saccade and adapted saccades) in which they had to localize a visual bar by verbal report and

ballistic pointing. Verbal responses were referred to a horizontal ruler that was displayed at beginning of each trial and disappeared at least 2 s before the appearance of a fixation spot (see [Figure 1](#)). The ruler (a series of equidistant 1 cm ticks see [Figure 1](#)) was displayed for 2 seconds and the subject could inspect it freely, without keeping fixation. The ruler was displayed at the same vertical position as the black dots used as fixation and saccadic targets. An experimenter recorded the verbal response on the computer.

In the “pointing response” trials, subjects had to point blindly (open-loop task) to the position of the bar by touching the corresponding area of a touch-screen with the index-finger tip of their right hand. Pointing responses were recorded by an add-on touch-screen (Keytec KTMT-1921USB) mounted onto the displaying monitor. Maximum error in position accuracy of the touch-screen was 3 mm and the activation force required was 50–120 g/cm². Subjects were explicitly instructed to respond as quickly and accurately as possible.

Both verbal and pointing responses were performed while the goggle-shutter was closed and the monitor was dark (see [Figure 1](#)). In those conditions, subjects were in complete darkness and could not perceive either the monitor frame or any other visual reference or their hands (open-loop condition). The goggles were driven directly by the visual stimulus generator in synchrony with the timing of stimuli presentation. Immediately after subject's response, the shutter goggles shifted back to open state and the monitor to the red background, to restore light adaptation. The conditions are such that during the appearance of the visual bar, about 100 ms after saccadic onset, several visual cues were available (the frame of the screen and the fixation dot). The subject was in complete darkness during the response.

The three different types of experiments were:

1. *Localization during fixation trials.* Subjects had to keep fixation on a black dot, which was displayed (in separate sessions) at 8° left, 1° right and 8° right of the center of the screen (only their gaze direction, and not their head direction, were eccentric) and that stayed on for the entire trial (in the verbal condition, the fixation dot appeared after 2 s that the ruler had disappeared). In addition, to mimic as closely as possible the visual stimulation delivered during the gain-decreasing condition of the *Adapted saccades* (see below), when the fixation dot was displayed at -8° (about 150 ms after the appearance of the fixation dot), another dot appeared at $+8^\circ$ and jumped after 150 ms to $+1^\circ$. In the second condition (fixation at $+1^\circ$), a dot that was initially displayed at -8° jumped to $+8^\circ$ and then disappeared after 150 ms, while in the third condition (fixation at $+8^\circ$), a dot was initially displayed at -8° and after 150 ms it jumped to $+1^\circ$. Finally the monitor went dark and the goggle shutter closed. The delay of the shutter from

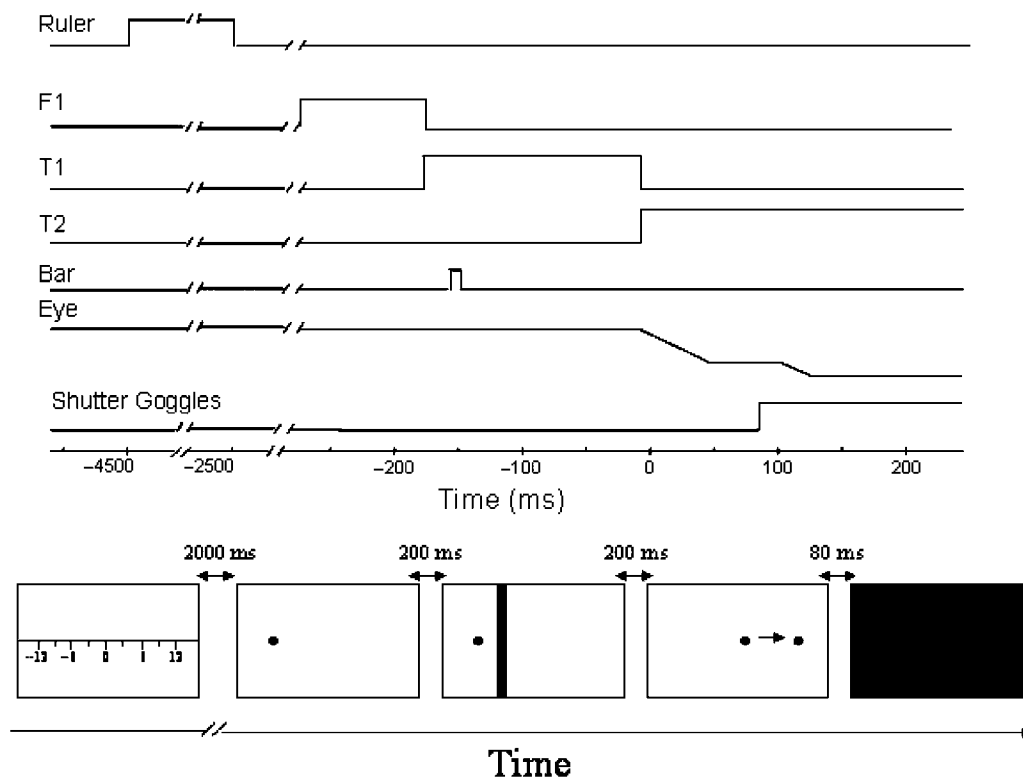


Figure 1. Temporal sequence of events for the adaptation trials. In the verbal condition, before the beginning of each trial, a graduated ruler was displayed for two seconds. At the beginning of the trial, the subject fixated F1 (which was displayed -8° (where 0 is defined as screen center)). When F1 disappeared, the first saccadic target appeared ($+8^\circ$ in the gain-decreasing condition and $+1^\circ$ in the gain-increasing condition; the figure shows the gain-increasing condition). Soon after saccadic onset, the target jumped to a new position ($+1^\circ$ in the gain-decreasing condition and $+4^\circ$ in the gain-increasing condition). Immediately after the execution of the saccade, vision was occluded by closing the goggle shutter.

the time of the displacement (equal to 80 ms) and the occurrence of the blue vertical bar (that was displayed 200 ms before the goggle shutter closed) were programmed to be as similar as possible to the adapted saccade sequence.

2. *Unadapted saccades localization.* After the ruler disappeared, a black dot (F1) was displayed 8° left of screen center. About 100 ms later, F1 disappeared and synchronously another black dot (T1) appeared (in separate sessions) at either $+1^\circ$ or $+8^\circ$, to which subjects saccaded. 80 ms after the target jump and always before the subject responded, the monitor went dark and the goggle shutter closed (see Figure 1). The blue vertical bar was displayed well before saccade onset (>150 ms) at random at all possible 29 positions.
3. *Adapted saccades localization.* With “adapted saccades” the saccadic target jumped to a new position during the execution of the eye-movement (the target step was triggered by the eye-position signal with a delay of about 10 ms). Subjects did not perceive the intrasaccadic target shifts and, after some 20 or so initial trials where they performed a corrective saccade, the saccadic amplitude gradually changed and approximated the second saccadic target, reaching

a constant level of adaptation after 40–60 trials (Figure 2). In separate sessions, subjects ran either gain-reducing adaptation trials (saccadic target stepped back from $+8^\circ$ to $+1^\circ$) or gain-increasing adaptation trials (saccadic target stepped forward from $+4^\circ$ to $+8^\circ$). The bar to be localized was displayed very early (>150 ms before saccade onset). Before each recording session, subjects ran saccade-only trials (no vertical bar was displayed) in order to gain a stable level of adaptation. Figure 2 shows a typical session to gain adaptation; despite the transient dark that could disorient the subjects they could acquire a stable level of adaptation in 40–60 trials, in agreement with previous studies (McLaughlin, 1967; Straube & Deubel, 1995; Watanabe et al., 2003). During these initial trials we did not measure localization. In any case, given that the bar presentation could be displayed in 29 different positions it would not be possible to evaluate the dynamics of the effects.

Data collection

For *Fixation and Unadapted saccade* conditions at least 250 trials were collected for each condition, while for

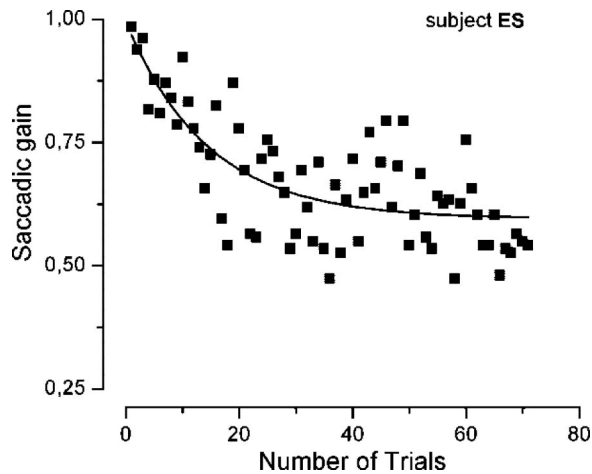


Figure 2. Saccadic gain (ratio of actual movement to distance to the first saccadic target) as a function of the number of trials in one experimental session, for one naïve subject (ES). The theoretical gain is equal to 0.56. Curve passing through the data is an exponentially decaying fit.

Adapted saccades more than 650 trials were collected for each condition. When comparing the effect of adapted saccades against saccades of the same amplitude, we accepted an adaptation trial response only if the amplitude of the primary saccade was 10% different than the distance between the initial fixation and the position of the second saccadic target, corresponding to a variation in gain of about 11% in both adaptation condition. Approximately 40% of adaptation trials were eliminated because they did not satisfy the restrictive criterion we adopted to judge trial validity. We also analyzed the response to all trials collected during adaptation independently of the eye landing position and verified that the strict criterion for the exclusion of the trials did not alter the pattern of the results (Figure 5). The same criterion (less than 10% error) was used for the normal saccades, eliminating about 2% of the trials.

For each trial, we stored the eye trace recorded by the eye-tracker and the presentation times for all the stimuli together with the subject's response. A later offline analysis allowed us to check more accurately the quality of saccade and computer's estimate of saccade onset.

Results

Fixation trials

Before assessing the effect of saccadic adaptation on pointing it is important to determine the accuracy of pointing during fixation and to compare it to the verbal localization in the same open-loop experimental conditions.

We measured these two localization performances for different gaze eccentricities corresponding to the positions of the initial fixation point, the first and the second saccadic target used in the gain-decreasing adaptation condition. Figure 3 shows an example of the results for

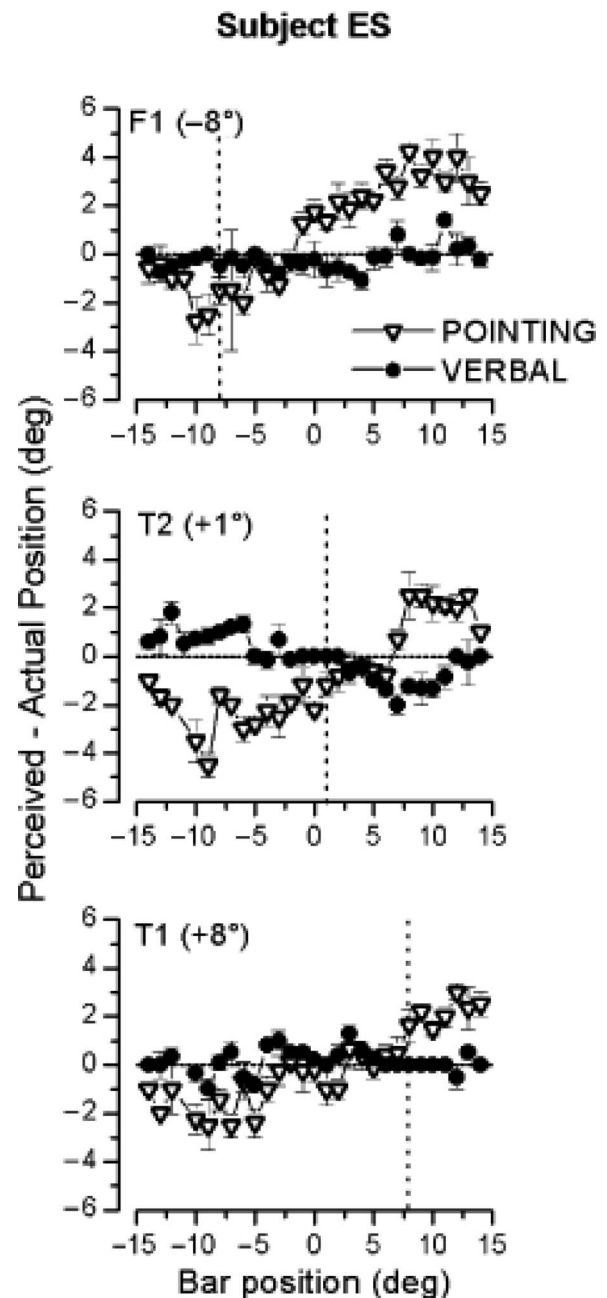


Figure 3. Mean localization of the flashed bars plotted as a function of the real position for three different gaze directions and for one representative subject (naïve ES). The upper panel reports the data obtained with gaze at -8° ; the middle panel at $+1^\circ$ and the lower panel at $+8^\circ$. Empty triangles show verbal reports, while filled circles the pointing data. For each real position, mean difference between perceived and actual position and standard error are plotted. Vertical dotted lines represent the position of the gaze.

one subject, both for the verbal and for the pointing localization for each gaze eccentricity. The upper row shows the data for fixation at -8° ; the middle row for T2 fixation (fixation at $+1^\circ$) and the bottom row for T1 fixation ($+8^\circ$). For all fixations the verbal report errors are small at maximum 2° , indicating near veridical performance. Similar results were obtained for the other subjects. Also the pointing localizations are very accurately distributed around a line with little variance (the correlation coefficient of the linear regression of the error are all higher than 0.993). However, for all fixations, all subjects made systematic localization errors overestimating eccentricity of the stimulus. The average slope of the error versus position for the 3 subject is 0.07 ± 0.03 , confirming previous data of (Beurze, Van Pelt, & Medendorp, 2006; Lewald & Ehrenstein, 2000). In general, for all subjects there was a variation of the pointing response with gaze, that is not evident in the verbal localization, indicating that the open-loop condition used in this study is able to dissociate between the two performances.

Pointing data collected in the saccadic condition may combine the localization processed during the pre- and post-saccadic fixation, making the study more difficult to interpret. In addition a comparison between verbal and pointing localization during saccade needs to take into account the different performance during fixation. For these reasons we compared for each modality the adaptation data with those of a saccade of the same amplitude as the adapted saccade.

Adapted versus Unadapted saccades

Two different adaptation conditions (gain-decreasing and gain-increasing) were run by the subjects in separate sessions. The observer fixated a black dot, displayed at -8° , keeping the head stable and centered on the center of the monitor (0°). As the fixation spot disappeared, the first saccadic target appeared (at $+8^\circ$ for the gain-decreasing condition and at $+4^\circ$ for the gain-increasing condition), to which subjects saccaded (see Figure 1). Triggered on-line with the saccade, the saccadic target jumped to a new position (backwards to $+1^\circ$ in the gain-decreasing condition and forwards to $+8^\circ$ in the gain-increasing condition), and after some initial trials (40–60 in the first recording session as shown in Figure 2, that could decrease to 10–30 in the subsequent sessions performed soon after in the same day), the subjects saccaded directly to the new position of the target without corrective saccades or being aware of the saccadic target jump. In the two unadapted conditions (9° saccades, from -8° to $+1^\circ$, and 16° saccades, from -8° to $+8^\circ$), no target jump occurred and the subject executed a single targeted saccade. The positions of the saccadic target of unadapted 9° and 16° saccades were same as the second saccadic targets of, respectively, gain-decreased and gain-increased

saccades. In all conditions (adapted or unadapted), pointing and verbal localization of a clearly visible bar, briefly displayed well before saccade onset (more than 150 ms: 193 ± 31 for AB, 230 ± 29 for MCM, 234 ± 24 for ES) in a random position were measured.

Figure 4 shows the results for all saccadic conditions for a naïve subject (ES) for both verbal and pointing localization, plotted as a function of physical location. An adaptation-specific effect occurs for both gain-decreasing and gain-increasing conditions: a wide range of stimulus positions (significantly exceeding the area between the two saccadic targets represented by the black arrows) is shifted in the direction of adaptation (as compared to the dotted equality line) both for verbal and for pointing localization (top row). There is no shift for normal unadapted saccades of approximately the same amplitude of the adapted ones (bottom row).

The localization data of Figure 4 for adapted saccades refer to saccades that landed in a radius of about 10% of the saccadic amplitude around the second saccadic target. While this allows us to compare directly the adapted data with those of normal saccade of the same amplitude, it opens the possibility that the effect reflects a bias in the sample, given that about 40% of the adapted trials were excluded. To test this possibility we also analyzed all the collected trials, and Figure 5 illustrates an example of the results for the pointing and gain-decreasing adaptation for subject AB. No significant difference in the mislocalization pattern was observed for any of the subjects or any condition: the maximum localization error was similar and largest around the position of the second saccadic target.

As previously observed by Henriques et al. (1998), and in agreement with the present data collected during fixation (Figure 3), eye position influences the ability to point correctly to the stimulus. For both adapted and unadapted saccades, the results show an overestimation of stimulus eccentricity (subject's eyes were approximately positioned at $+1^\circ$ for the gain-decreasing condition and for the 9° saccade, while they were at about $+8^\circ$ for the gain-increasing condition and for the 16° saccade), especially for more peripheral bars displayed at positions left of -5° . In order to separate the effects of adaptation from these effects related to gaze eccentricities and saccades, we plotted data of the adapted saccades against those obtained during normal unadapted saccades. These plots are particularly useful to highlight only localization differences that can be specifically ascribed to saccadic adaptation.

Figures 6 and 7 show the major results for gain-decreasing and gain-increasing adaptation condition respectively, for three different subjects. The upper panel shows the data obtained in verbal-response conditions; the lower panel for pointing-response conditions. Within each panel, mean and standard error of the localization during adaptation are plotted as a function of mean and standard error of the localization for unadapted saccades. Adapted and unadapted saccades are matched according to their

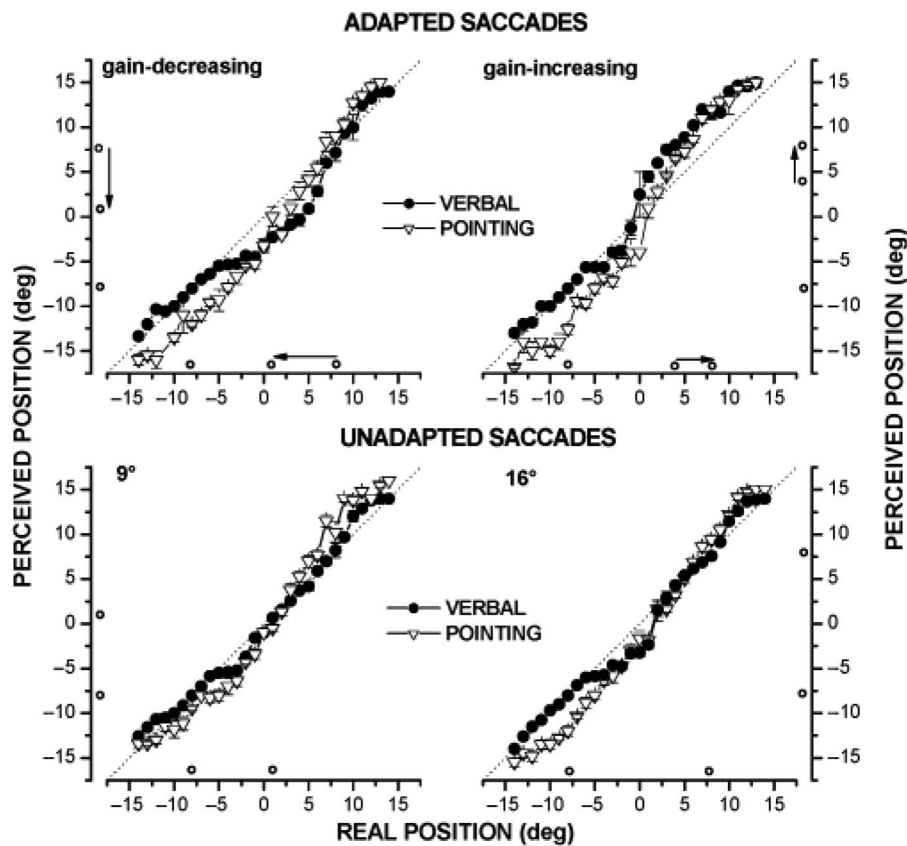


Figure 4. Mean localization of flashed bars displayed before than 150 ms saccadic onset plotted as a function of real position for one subject (ES). The upper panel plots data from the two adaptation condition (gain-decreasing and gain-increasing), the lower panel data from the two normal unadapted saccadic conditions (of matched amplitude 9° and 16°). Empty triangles for the pointing reports and filled circles for the verbal reports. Bars plot standard error of the mean. Empty circles on the axis indicate, for each condition, the position of fixation, first and second saccadic targets. Black arrows indicate the direction of adaptation. Dotted line is the equality line.

amplitude (9° and 16° saccades respectively). Empty circles on the axis show the position of the initial fixation spot and of the saccadic targets. Data points that diverge from the equality line (dotted line) indicate that the bar is localized differently in the condition of saccadic adaptation compared to the condition of unadapted saccades.

For both gain-decreasing and gain-increasing adaptation, and for both response types, there is a wide range of positions that are localized differently than in normal saccades (all points away from the equality line of Figures 6 and 7). The verbal data replicate well the previous results showing strong alteration of the space around the two saccadic targets in the direction of the adaptation (Awater et al., 2005). During adaptation, bar localization is shifted towards the second saccadic target, producing data points that are below the equality line for the gain-decreasing adaptation and above the equality line for the gain-increasing adaptation. The amplitude of the shift is, on average, very similar for the two adaptation conditions, with peaks of mislocalization in the range 4.5°–5° for all subjects. Similar effects are also evident for the localization by pointing, although the effect is distributed over a large range of positions.

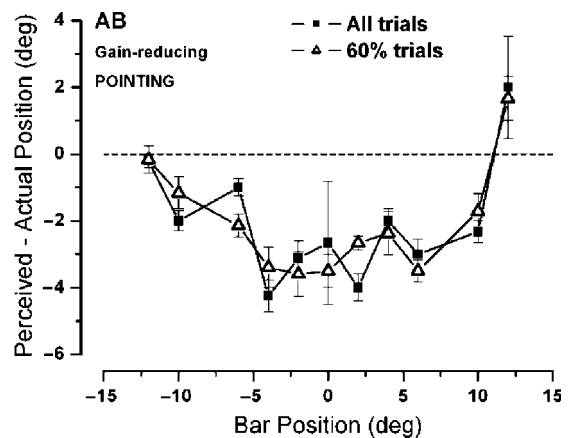


Figure 5. Mean difference between perceived position (estimated by a pointing response) and actual position as a function of the bar position for one representative subject (AB) in two sets of adaptation data. The means described by filled squares were calculated including all the adaptation trials, while for empty triangles the trials that did not satisfy the restrictive criterion adopted to judge trial validity (see Data collection) were discarded (about 40%).

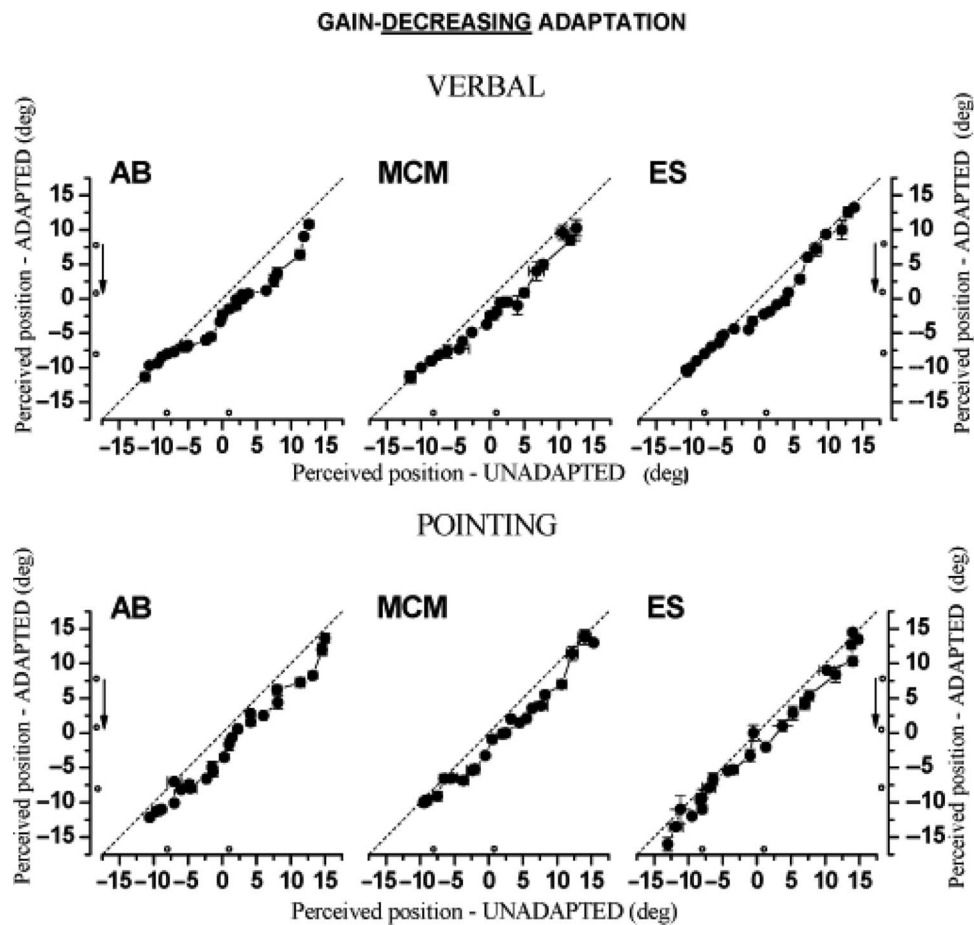


Figure 6. Mean perceived position of flashed bars for the gain-decreased adapted saccades plotted as a function of mean perceived for the normal 9° unadapted saccades for three different subjects for verbal (top) and pointing (bottom) reports. In both conditions (adapted and unadapted), bars were displayed more than 150 ms before saccade onset. Standard errors for both conditions are also plotted (vertically for the adaptation condition, horizontally for the unadapted one). Empty circles show, for each condition, the position of fixation, first and second saccadic targets. Black arrows indicate the direction of adaptation. Dotted line is the equality line.

The mean differences in localization between adapted and unadapted saccades was significantly different from zero for each individual subject as assessed by a one-sample t -test for the verbal and pointing condition in the gain decrease adaptation (see Table 1). The difference is also highly statistically significant for the gain-increase adaptation for all subjects for the verbal reports, but significant only in two subjects for the pointing condition and not for subject ES. However the test was performed for all the 29 positions and for the subject ES the effect is restricted to a smaller region. In addition for this subject, the positions close to the initial fixation were shifted in the opposite direction of the adaptation, resulting in a small and not-significant average shift.

Figure 8 describes the localization shift (averaged among three subjects) as a function of bar position for all experimental conditions. This shift is defined, for each bar position, as the mean difference in localization between perceived and actual position of the bar. For both gain-decreasing and gain-increasing adaptation, the mislocalization is stronger in a region around the two

saccadic targets. The overall pattern of results is similar for the two tasks. Statistical t -tests performed independently for each position (using a bootstrap method: Efron & Tibshirani, 1993) show that the difference between the two tasks is statistically significant only in few positions. The difference between verbal and pointing was significant ($p < 0.05$) for the gain-increase in the range from -3 to 2 and for positions 7, 10 and 12; for the gain-decrease in the range from 1 to 3.

Discussion

The main aim of the present study was to investigate whether an adapted eye-position signal causes a recalibration of the spatial metrics used to localize an object in space, independently of the mode of response.

The first experiment replicated the already well known finding that the eye-position signal influences localization

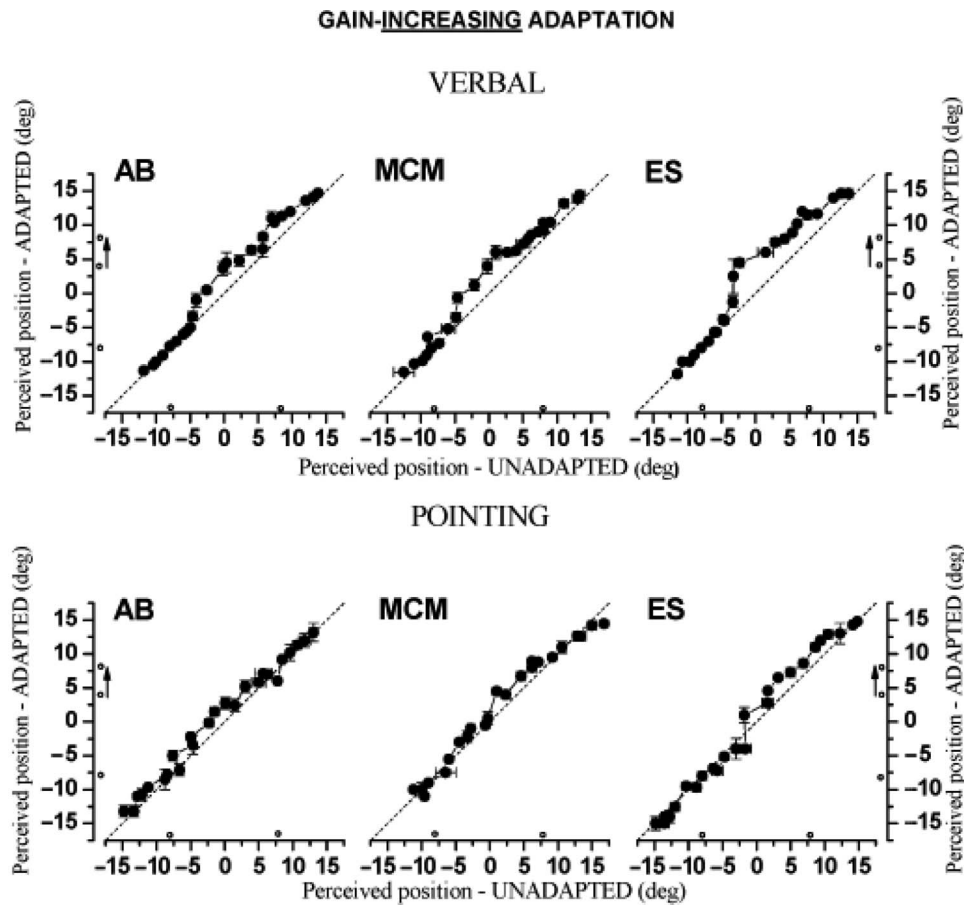


Figure 7. Mean perceived position of flashed bars obtained during gain-increased adapted saccades plotted as a function of mean perceived position of flashed bars obtained during normal 16° unadapted saccades for three different subjects. In both conditions (adapted and unadapted), bars were displayed more than 150 ms before saccade onset. Standard errors for both conditions are also plotted (vertically for the adaptation condition, horizontally for the unadapted one). In the upper panel, verbal report data are plotted, while, in the lower panel, we report pointing response data. Empty circles describe, for each condition, the position of fixation, first and second saccadic target. Black arrows describe the direction of adaptation. Dotted line is the equality line.

performances when assessed through a goal-directed pointing movement during fixation (Beurze et al., 2006; Bock, 1986; Enright, 1995; Henriques & Crawford, 2000; Lewald & Ehrenstein, 2000) and after a saccade (Henriques et al., 1998). There was a general tendency for the pointing response to overestimate the distance between the stimulus and gaze direction and, in agreement with

previous studies, the pattern of results is consistent with the idea that an eye-centered frame of reference is used in pointing task. In the same condition we were able to show a dissociation between action and perceptual localization suggesting that space is coded differently for the two tasks: localization was nearly veridical with a purely perceptual judgment for all gaze direction, but very poor

Subject	Gain-DECREASING						Gain-INCREASING					
	Verbal			Pointing			Verbal			Pointing		
	Mean	<i>t</i>	<i>p</i>	Mean	<i>t</i>	<i>p</i>	Mean	<i>t</i>	<i>p</i>	Mean	<i>t</i>	<i>p</i>
AB	-2.28	-6.7	<0.0001	-2.66	-1.27	<0.0001	1.61	5.46	<<0.0001	1.12	5.07	<0.0001
MCM	-2.07	-7.35	<0.0001	-1.9	-7.7	<0.0001	1.87	6.93	<<0.0001	0.72	2.53	<0.01
ES	-1.26	-4.35	<0.0001	-1.76	-7.19	<0.0001	2.17	5.03	<<0.0001	0.51	1.57	0.06

Table 1. The mean differences in localization (verbal and pointing) between adapted and unadapted saccades, both in the gain-decreasing condition and in the gain-increasing condition, are reported for three different subjects. *t*-test- and *p*-values for each condition are also shown.

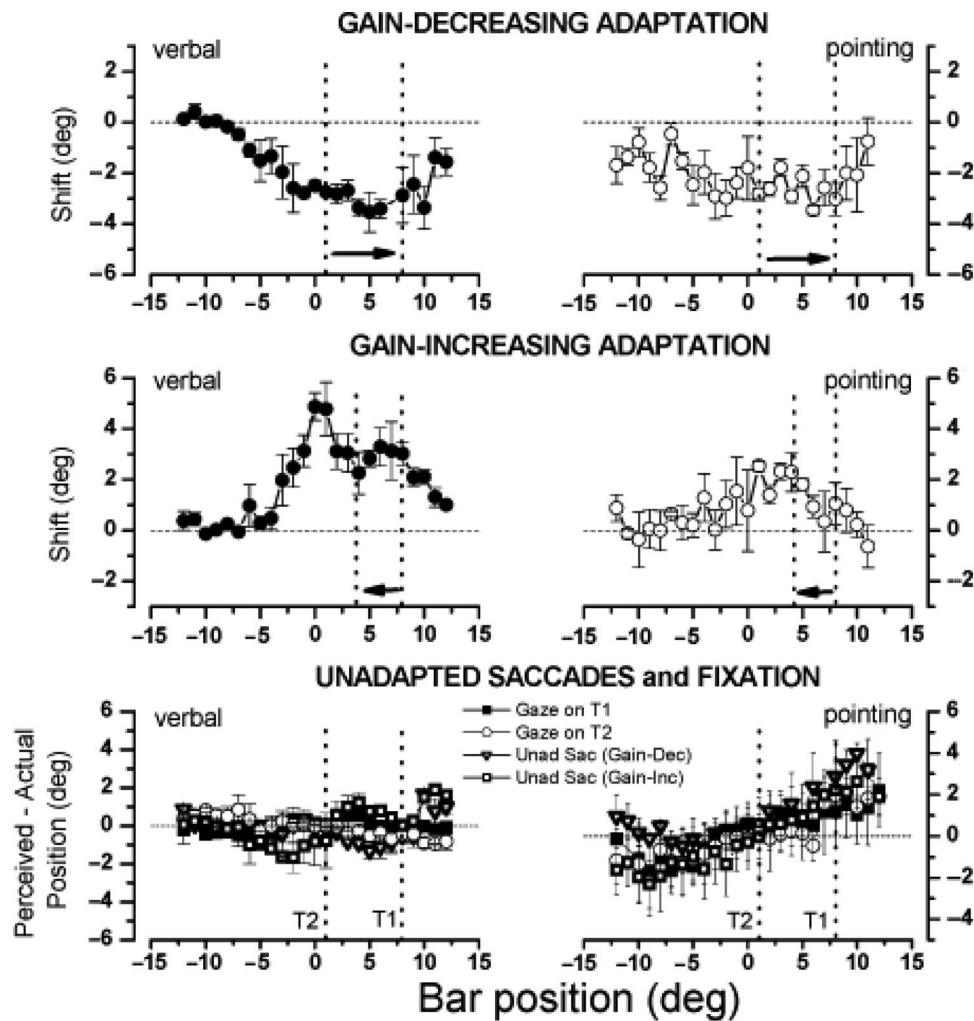


Figure 8. Localization shift (averaged among three subjects) plotted as a function of actual bar position for all the experimental conditions. Data from gain-decreasing are reported in the upper panels; gain-increasing adaptation in the intermediate panels; unadapted saccades and fixation in the lower panels. For the adaptation conditions (upper and intermediate panels), the shift for each position is calculated as the mean differences in localization between adapted and unadapted saccades. For fixation and unadapted saccades (lower panels), the shift is calculated as the difference between perceived and actual position of the bar. Left panels show the shift for verbal reports, right panels show the shift for pointing responses. In the lower panels, filled squares show the shift when subjects fixated 8° right of the centre of the screen, filled circles when subjects fixated 1° right of the centre of the screen; empty triangles show the shift for 9° unadapted saccades, empty squares for 16° unadapted saccades. Vertical dotted lines indicate, for each condition, the position of the first and the second saccadic target (for the fixation conditions, they indicate the position of the subjects' gaze). Black arrows indicate the direction of the target jump.

and grossly distorted for a manual ballistic movement. There may be several explanations of the accurate perceptual localization. If perceptual localization is accomplished by comparing the position of the actual visual excitation with a spatial representation stored in memory, an eye-position signal could alter both by the same degree, resulting in the annulment of the deformation. Another explanation relies on the ability of the “perceptual” visual system to locate objects with relative rather than absolute distances, as already advanced by Goodale and collaborators (for review see Goodale & Milner, 1992; Goodale & Westwood, 2004) and by Burr,

Morrone, and Ross (2001b) by Morrone et al. (2005) for peri-saccadic localization. In the present experiment, relative distances between the fixation spot, saccadic target and the frame of the monitor, all clearly visible when the bar was presented, may help in achieving a nearly veridical localization during fixation and during normal saccade.

Independently of the possible mechanisms that mediate the dissociation, for the goals of this study it is essential to show that in the same condition it was possible to generate a different pattern of localization for action and perception. Only if there were a dissociation between fixation and

normal saccades would it be possible to address the question of whether adaptation induces the same effect in the two different representations. The main result of this study is that saccadic adaptation influences both perceptual and action space representation, with similar deformations for both gain-decreasing and for gain-increasing conditions. A related finding is that the alterations induced by adaptation are not homogenous across space, but stronger in the region around the two saccadic targets.

Unlike previous experiments investigating the transfer of saccadic adaptation to other motor modalities, we tested the spatial deformation over a wider range of spatial positions. In the post-adaptation phase, both Bekkering et al. (1995) and Kröller et al. (1999) found an alteration of the goal-directed hand movement for regions close to the saccadic target, but the effects were usually small, and only statistically significant when the pointing and eye-movement were coupled. Both studies concluded that saccadic adaptation is a phenomenon restricted to the oculomotor system, and the transfer to other movements too weak to be important in motor coordination. In the present experiment, the pointing and the eye movements were never simultaneous, neither in the adaptation training nor during the test trials. Subjects were required to point to the perceived position of the stimuli only after completing the saccadic eye movement. The vertical bars could appear at random at one of twenty nine possible locations, covering a viewing angle of approximately 30° (the distance between contiguous bars was 1°), eliminating the predictability of target localization. In these conditions we were able to show a strong alteration of the pointing localization, demonstrating a substantial transfer of adaptation. However, the alteration was always much smaller than the variation in gain of the saccade and stronger around the saccadic targets, indicating that the transfer was not complete.

The present results show comparable patterns of errors for the perceptual and the goal-directed movement. The transfer of saccadic adaptation to other motor outputs could be mediated either by a perceptual remapping of the visual world, or could operate at a common output level of the motor system (Bekkering et al., 1995). Previous studies have shown an alteration of the perceptual localization by saccadic adaptation. Moidell and Bedell (1988) found a limited but significant effect of adaptation on a distance judgment task performed by the subjects during fixation and after saccadic adaptation. Bahcall and Kowler (1999) also demonstrated an influence of saccadic adaptation on perceptual localization for position around the saccadic target. They associated the error to a mismatch between the actual eye movement and the intention-to-move signal, concluding that the eye-position signal which is used to recalibrate the spatial maps is at higher levels than the adaptive sites. Awater et al. (2005), using a paradigm similar to that adopted in our experiment, measured visual localization performance through a verbal report for pre-saccadic stimuli under conditions of saccadic adaptation

and found a significant shift of the perceived positions in the direction of adaptation, confirming Bahcall and Kowler (1999) results. However, the stimuli which were affected by what they called a “long-lived perceptual shift” in the direction of adaptation were mainly those displayed in an area between the two saccadic targets, in agreement with the present data (see Figure 8). Awater et al. (2005) shows that the perceptual mislocalization is present only if the subject is in an adapted state and is performing a saccade. Catch trials, where visual reference associated with the saccadic target were dramatically reduced (the first saccadic target disappeared and no secondary saccadic target were presented), show the same pattern of mislocalization; on the other hand fixation trials, intermingled with adapted saccade trials, show veridical localization. In the present study we did not attempt to reproduce the effect with catch trials, given the higher complexity of the open-loop apparatus and the transient dark that was disturbing and disorienting for the subjects. However, given that experimental similarity between these studies and the similarity in the adaptation level achieved (compare Figure 2 with Figure 1 of Awater et al., 2005), it is highly probable that also in this study the mislocalization is specific to the adaptation state.

If the effect is specific to adaptation, why should it be limited to a small region and not to all space? The reason for this is far from clear. Post-saccadic visual references are considered important in stabilizing vision and reducing errors (Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 2002; Lappe, Awater, & Krekelberg, 2000). In many trials of the present experiments the bar is presented while the fixation spot is still present and the relative distance between the two may help localization for positions around fixation, both in the adapted and in unadapted state. Although the unhomogeneity of the mislocalization may be at least partially influenced by the presence of visual cues, the results indicate the presence of a compensatory mechanism for the adaptation. If the metrics of the perceptual space were actually recalibrated by an intention-to-move signal, as proposed by Bahcall and Kowler (1999), its effect might be stronger in the more important visual region around the postsaccadic fixation than for more peripheral positions, indicating a warping of the spatial metric rather than a rigid shift.

In many conditions it has been possible to demonstrate the existence of a separate perceptual and action representation of visual space (Burr et al., 2001b; Goodale & Milner, 1992; Goodale & Westwood, 2004; Morrone et al., 2005). In particular, the dissociation is very strong for peri-saccadic stimuli that are localized nearly veridically for pointing, but subject to strong deformation for verbal report. Interestingly here we found that the difference in the effect of adaptation between verbal and pointing localization, if present, is small. This would suggest that adaptation is altering in parallel both the perceptual and the action representation of space, showing a high

plasticity not only of the perceptual system but also of the motor system that may be important for visual motor coordination.

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