BRAIN RESEARCH 1172 (2007) 32–39

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Motor space structures perceptual space: Evidence from human saccadic adaptation

Thérèse Collins[a,*], Karine Doré-Mazars[a], Markus Lappe[b]

[a]Laboratoire de Psychologie et Neurosciences Cognitives, Paris Descartes University and CNRS, FRE 2987, 71 Avenue E. Vaillant, 92 774 Boulogne-Billancourt, France
[b]Department of Psychology II, Westfälische Wilhelms University, Fliednerstr. 21, D-48149 Münster, Germany

ARTICLE INFO

Article history:
Accepted 25 July 2007
Available online 3 August 2007

Keywords:
Saccade
Adaptation
Localization
Perception

ABSTRACT

Saccadic adaptation is the progressive correction of systematic saccade targeting errors. When a saccade to a particular target is adapted, saccades within a spatial window around the target, the *adaptation field*, are affected as a function of their distance from the adapted target. Furthermore, previous studies suggest that saccadic adaptation might modify the perceptual localization of objects in space. We investigated the localization of visual probes before and after saccadic adaptation, and examined whether the spatial layout of the observed mislocalizations was structurally similar to the saccadic adaptation field. We adapted a horizontal saccade directed towards a target 12° to the right. Thirty-eight saccades towards the right visual hemifield were then used to measure the adaptation field. The adaptation field was asymmetric: transfer of adaptation to saccades larger than the adapted saccade was greater than transfer to smaller saccades. Subjects judged the localization of 39 visual probes both within and outside the adaptation field. The perceived localization of a probe at a given position was proportional to the amount of transfer from the adapted saccade to the saccade towards that position. This similar effect of saccadic adaptation on both the action and perception representations of space suggests that the system providing saccade metrics also contributes to the metric used for the perception of space.

© 2007 Elsevier B.V. All rights reserved.

1. Introduction

When systematic targeting errors occur in the oculomotor system, they are progressively corrected for by a process called saccadic adaptation. Adaptation can be observed in patients suffering from extraocular muscle dysfunction: the initial dysmetria disappears after a few days and patients then recover normal targeting capabilities (Abel et al., 1978). A similar phenomenon is observed in monkeys whose extraocular muscles have been partially lesioned (Optican and Robinson, 1980). Short-term saccadic adaptation can be studied non-invasively in the laboratory by surreptitiously displacing the target during the saccade directed towards it, thus mimicking a targeting error when the eye lands (McLaughlin, 1967). Such behavioral adaptation is specific to the adapted amplitude and direction, as the transfer of the adaptation of a given saccade to other saccades depends on their difference with the adapted saccade (Frens and van Opstal, 1994). The spatial window surrounding the adapted saccade inside which the adaptation transfers to other saccades is called the *adaptation field*. In monkeys, the adaptation field is asymmetric around the adapted saccade

---

[*] *Corresponding author.*
E-mail address: therese.collins@univ-paris5.fr (T. Collins).

0006-8993/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2007.07.040

vector: smaller saccades are less affected than larger ones (Noto et al., 1999). Because of the similarity with movement fields of superior colliculus and frontal eye field neurons, this was interpreted as pointing towards an implication of these brain areas in the adaptive process. The human saccadic adaptation field remains to be investigated and is a matter of debate because of rate (Deubel et al., 1986) and specificity (volitional versus reactive saccades; Deubel, 1995; Fuchs et al., 1996; Collins and Doré-Mazars, 2006; Alahyane et al., 2007) differences with monkeys.

Saccadic adaptation seems to affect the perceived localization of visual objects (Bahcall and Kowler, 1999; Awater et al., 2005). Previous studies tested one to four probes in the vicinity of the adapted saccade target and observed that localization depended on the adapted state of the saccade. Interestingly, the shift of localization occurred for probes presented more than 100 ms before the saccade, suggesting that the localization shift was not the result of the compression of visual space towards the saccade endpoint, which occurs at shorter delays before saccade onset (Ross et al., 1997; Awater et al., 2005) but would rather concern a higher level representation of the target. These results pose the intriguing question that saccadic adaptation might be accompanied by a distortion of perceived space. If this were the case, the distortion might present the same asymmetry as the adaptation field.

We investigated the influence of saccadic adaptation on the localization of visual probes presented both within and outside of the adaptation field of a 12° rightward horizontal saccade. We measured the adaptation field by testing the transfer of the 12° horizontal saccade adaptation to 38 saccades with different amplitudes and directions. We then compared the adaptation field to the localization of visual probes presented briefly before the saccade. Subjects localized the probes after their saccade by clicking on the position they thought the probe had appeared in with a mouse pointer. Localization was tested in three conditions. In one of these, the localization judgment was made with the saccade target present on the screen. Therefore, subjects performed the localization judgment in the presence of a visual reference. In the second condition, the saccade target was extinguished during the saccade. Therefore, when the saccade landed, no visual stimuli were present on the screen, and subjects performed the subsequent localization judgment without post-saccadic visual references. In the third condition, subjects had to maintain fixation throughout the trial, and all visual events occurred after delays comparable to the two other localization conditions (see Fig. 1a and Experimental procedure). Our hypothesis was that if saccadic adaptation is accompanied by a distortion of visual space, it should have the same spatial boundaries as the adaptation field. Furthermore, the presence of post-saccadic visual references should also contribute to localization judgments.

2. Results

2.1. Saccade latency

All saccades were volitional in that they aimed for a permanent stimulus. Indeed, the fixation cross and the saccade target appeared simultaneously and overlapped for 600–800 ms. Subjects were to execute their saccade only when the fixation cross disappeared. Average saccade latency was 208 ± 29 ms. Pre-adaptation and adaptation did not differ from each other ($F<1$). Importantly, there was no difference between the three conditions ($F<1$) in which subjects made saccades (saccades to the 12° target, saccades to the same

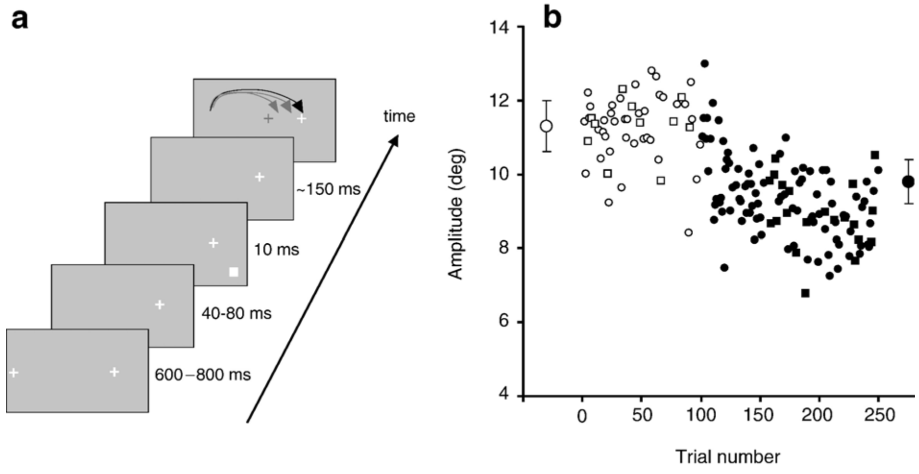

Fig. 1 – (a) Procedure. Subjects fixated on the fixation cross to the left. The go-signal for the saccade (disappearance of the fixation cross) occurred 600–800 ms later. 40–80 ms after this go-signal, about 150 ms before saccade onset, the probe flashed for 10 ms. Subjects then executed their saccade. Depending on condition and phase, during the saccade the saccade target could step back by 4° (shown here as a gray cross), disappear, or remain at the initial position. Example saccades are given for the pre-adaptation (black arrow) and adaptation phases (gray arrows). (b) Time course of the 12° saccade adaptation in one subject (S2) and one session. Each data point represents one saccade. The large symbols to the left and right of the individual data with error bars represent the average and standard deviation over all subjects and sessions. Both trials in which the saccade target remained on after the saccade (○) and those in which the saccade target was extinguished during the saccade (□) are shown. Open symbols: pre-adaptation, trials 1–100. Filled symbols: adaptation, trials 101–250.

target during which the target disappeared, saccades to any of the other 38 targets).

2.2. *Characteristics of saccadic adaptation*

In the pre-adaptation condition, the average amplitude of the saccade directed to the target located 12° to the right was 11.3 ± 0.7°. After 50 adaptation trials during which the target stepped back by 4°, the amplitude was significantly reduced to 9.8 ± 0.6° ($p<0.02$). Fig. 1b presents an individual time course of adaptation. The average amount of adaptation of the 12° saccade was 13 ± 0.5% (%gain change: $[(\text{Amplitude}_{\text{PRE}} - \text{Amplitude}_{\text{ADA}})/\text{Amplitude}_{\text{PRE}}] \times 100$). The amount of adaptation did not depend on whether the target remained on or was extinguished during the saccade ($F<1$).

2.3. *Saccadic adaptation field*

Subjects made saccades towards 39 different targets with different horizontal or vertical components, amplitudes and directions than the adapted 12° horizontal saccade. In the pre-adaptation phase, saccades slightly undershot the targets. After 50 adaptation trials, endpoints shifted leftward. The extent of the adaptive shift is measured by the distance between the pre-adapted and adapted saccade endpoints (i.e., the length of the adaptation ‘tail’ in Fig. 2a).

We assessed the effect of the 12° horizontal saccade adaptation on neighboring saccades of different amplitudes and directions by calculating the % adaptation transfer from the adapted 12° saccade to each of the other 38 saccades. First, the gain change for each saccade was calculated as for the adapted 12° saccade. Then, this gain change was compared to the gain change of the 12° adapted saccade: ((%gain $\text{change}_{\text{SACCi}}$/13%) × 100). Transfer of adaptation depended on the distance separating the tested saccade from the 12° adapted saccade. Globally, transfer decreased with increasing distance to the 12° adapted saccade. However, this decrease in transfer was asymmetric: the decrease in transfer to saccades larger than 12° was less pronounced than to saccades smaller than 12°. To quantify these observations in a manner comparable to previous reports on monkey adaptation fields (Noto et al., 1999), the amount of transfer was plotted for saccades sharing the same horizontal or vertical component as the 12° adapted saccade (Fig. 2b). A steeper drop in transfer for saccades smaller than 12° than for saccades larger than 12° can be seen, but no such asymmetry was observed along the vertical axis.

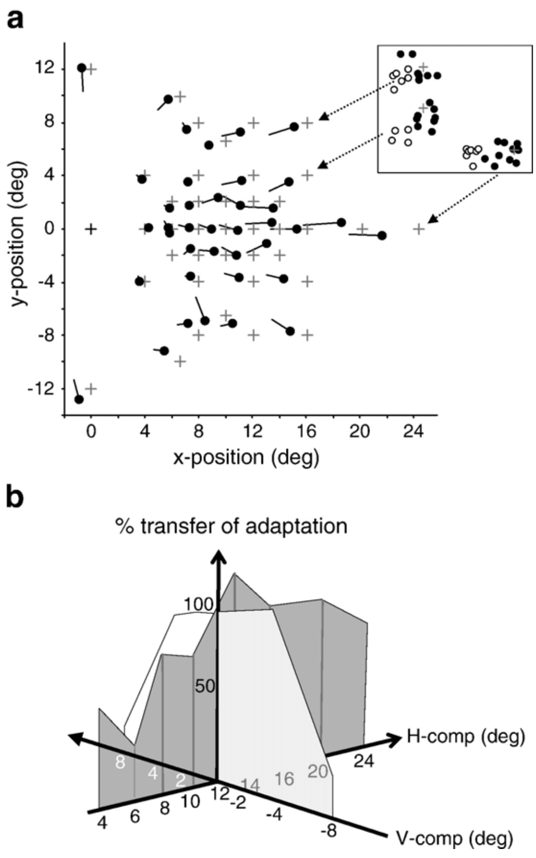

Fig. 2 – (a) Saccade endpoints in pre-adaptation (•) and adaptation (tip of the black tail) phases. Each data point corresponds to the average across the 4 subjects. (+) Saccade targets; (+) fixation point. Inset: individual data (Subject 1) for three example saccade targets (open symbols: adaptation). (b) Adaptation transfer from the 12° horizontal saccade to saccades sharing the same horizontal (gray) or vertical (white) component. Each data point corresponds to the average across the 4 subjects.

2.4. *Probe localization*

When visual references were available after the saccade, we hypothesized that subjects would use them to estimate the localization of objects presented before the saccade. The preponderant role of post-saccadic visual references in localization has been suggested by the landmark effect (Deubel, 2004). When a visual object changes position during the saccade, subjects do not notice because of saccadic suppression of displacement (Bridgeman et al., 1975), but when the object is no longer visible when the eye lands, position changes are detected (Deubel et al., 1996). If a continuously visible object changes position during the saccade and another does not change positions but is blanked, the permanent object will be seen as stationary and the blanked object as moving (Deubel et al., 1998). Thus, objects present after the saccade would serve as landmarks and other objects would be realigned accordingly. In the present experiment, the saccade target at (12°, 0°) could act as a landmark. In the adaptation phase, other visual objects not present after the saccade (i.e., the probe) could be realigned according to the new target position, 4° to the left of the pre-saccadic position. As seen in Fig. 3a, during the adaptation phase, over the 39 probe positions, judgments were on average shifted leftwards by 2.2° relative to the pre-adaptation phase (significantly different from 0, Student’s *t*-test, $p<0.01$).[1]

---

[1] We did not expect the judgment shift to be as large as the back-step of the saccade target (4°). Indeed, previous reports about the landmark effect (Deubel, 2004) have shown that the apparent displacement of a probe is smaller than that of the post-saccadic object whose displacement drives the illusion.

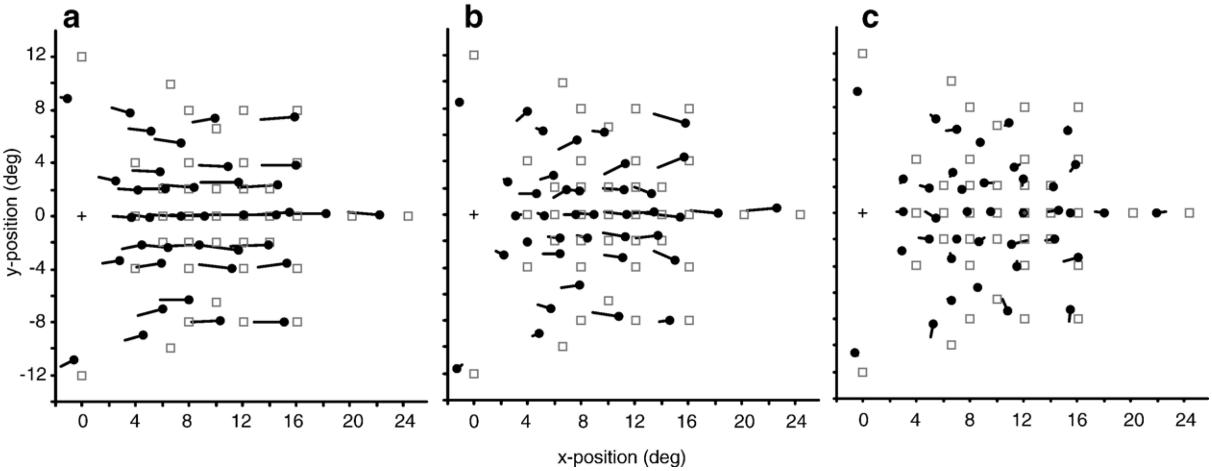

Fig. 3 – Localization judgments (a) with and (b) without the post-saccadic visual reference provided by the saccade target, and (c) in the fixation condition. Each data point corresponds to the average across the 4 subjects. (□) Probe positions. All other conventions as in Fig. 2a.

When visual references were not available after the saccade, during the adaptation phase localization judgments shifted leftwards on average 1.5° relative to pre-adaptation (significantly different from 0, Student's *t*-test, $p<0.05$), not as much as in the previous condition although the difference just failed to reach significance ($p>0.06$). The shift of localization judgments appears to be spatially non-uniform (Fig. 3b), with a larger localization shift for probes to the right of the 12° saccade target than for those to the left. This spatial heterogeneity of localization shift size appears similar to the spatial heterogeneity of adaptation transfer (Fig. 2a). For example, the leftward shift of localization judgments for the probe at the same position as the saccade target was 1.8±0.5°. The probe 2° to the right was shifted leftward by 2.0±0.2° while the probe 2° to the left by only 1.2±0.5°. The probe 2° above the saccade target position was shifted by 1.5±0.3°, and the probe 2° below 1.4±0.5°.

To quantitatively compare the amount of localization shift to the amount of saccadic adaptation, Fig. 4 plots the correlation between the two effects (i.e., between the amplitude of the "adaptation tails" in Figs. 2a and 3b). There was a positive correlation between the size of the amplitude reduction of a saccade to a given position and the size of the shift in localization judgment for a probe at the same position. This suggests that the estimated probe location depended in part on the metrics of the saccade that would move the eyes to that probe (as measured in the saccade condition), even when that saccade was not the one actually made at the time of localization. Such motor targeting information might also be used in the condition where subjects localized with post-

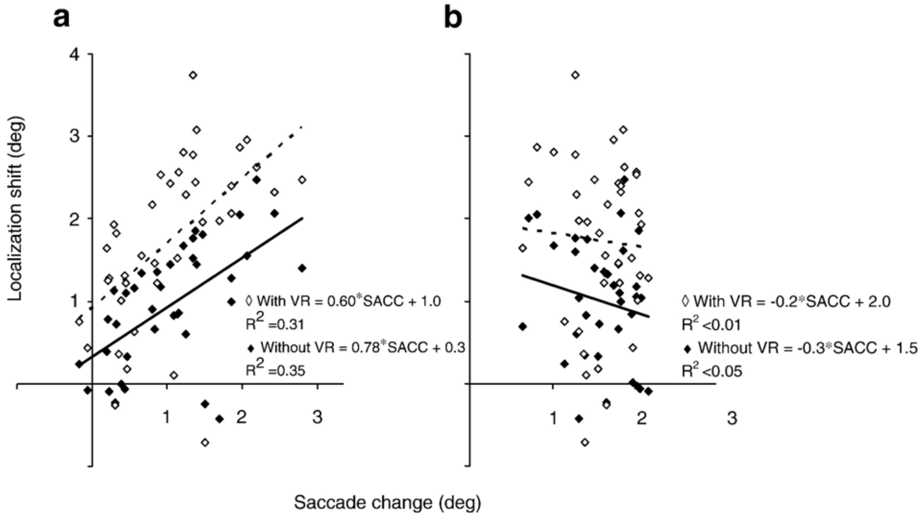

Fig. 4 – Correlation between the size of the saccade change (SACC) and the size of the localization shift, in degrees of visual angle, for trials in which subjects localized with (◊, dashed line) or without (♦, full line) visual references (VR). Each data point corresponds to the average over the 4 subjects for one tested position. (a) Size of the change of saccades made to each tested position in the saccade condition. (b) Size of the change of the saccades towards the 12° target executed during the localization trials.

saccadic visual references. Indeed, there was a similar correlation between localization shift and the size of the adaptive change, but an additional localization judgment shift of 0.7° was also observed — corresponding to the effect of the post-saccadic visual reference pulling the localization judgment to the left. Indeed, the leftward shift of localization judgments for the probe at the same position as the saccade target (12° to the right) was 3.7 ± 0.3°. This shift is closer to the size of the backward step of the target than to the amount of adaptation of the saccade aimed at this target, suggesting the use of exocentric cues. However, the correlation shown in Fig. 4a suggests that size of the localization shift also depended on the amount of adaptation of the saccade made towards the target occupying the same position as the probe.

Both the sizes of the localization shift and that of the adaptive saccade change were correlated with probe position. In order to make sure that the correlation between the localization shift and the adaptive saccade change was not artifactual result of their independent correlation with probe position, we fitted the localization shift data with a multiple regression model including probe position and saccade change as regressors. The total variance accounted for by the multiple regression model was 68 and 48% in the localization conditions (with and without post-saccadic visual references, respectively). In both conditions, the amount of variance uniquely accounted for by the amount of adaptive saccade change was significant (partial $R^2 > 35\%$; $ps < 0.005$). Therefore, it appears that the adaptive saccade change had a unique effect on localization shift that cannot be accounted for by a confound with probe position.

Another possible source of information that could be used for localization was the executed eye movement. In the localization trials subjects always performed a saccade towards the target 12° to the right, and never a saccade to the probe. Visual objects could be localized after a saccade by subtracting the executed saccade vector from the memorized probe position; the amount of localization shift would then depend on the amount of 12° saccade adaptation. Fig. 4b plots the correlation between the localization shift and the amount of saccadic adaptation of the 12° saccade. This factor accounts for less than 5% of the localization shift variance.

In the fixation condition, subjects were instructed to maintain their gaze on the fixation cross throughout the trial. The target at (12°, 0°) was continuously visible. Fixation was considered broken if subjects made a saccade any time during the trial up to 100 ms after the appearance of the mouse pointer but were allowed to view freely while making their localization judgment, as in the other conditions. Fixation was maintained successfully in 57% of trials. The difference between pre-adaptation and adaptation localization judgments was 0.1°, which was not significantly different from 0 (Student's *t*-test, $p > 0.1$).

Because the perceived localization of the probe was affected by saccadic adaptation, it could be argued that the perceived position of the mouse pointer was also influenced, and that the shift in probe localization actually resulted from the effect of adaptation on the mouse pointer. Two arguments point away from such an interpretation. First, the shift of perceived localization occurred for a probe that was no longer visible when subjects made their judgment. On the contrary, the mouse pointer was continuously visible. We hypothesize that when visual references are available, subjects use them to localize objects, as we showed in both the condition in which subjects localized with visual references and the fixation condition. Indeed, subjects were free to move their eyes as soon as the mouse pointer appeared on the screen and were most often fixating on or near the pointer when they made their localization judgment. If the mouse pointer had been affected by adaptation, this effect should have been visible in the fixation condition as well. Second, if the mouse pointer had been affected by adaptation, we would have expected not to observe a shift of localization judgments on the probe. When subjects performed their judgment, they placed the perceived position of the pointer on the location they thought the probe had appeared in. If the mouse pointer had been affected by the adaptation in the same way as the probes, this effect should have exactly cancelled out the shift of localization judgment on the probes. This was clearly not the case.

3. Discussion

We evoked saccadic adaptation for a 12° rightward saccade and modified the amplitude of surrounding saccades by adaptation transfer. We first sought to fully describe the spatial extent of the amplitude modifications. Then, we examined the effect of these modifications on the localization of different probes placed within this space and showed that they were accompanied by changes in the apparent localization of visual probes.

The results provide evidence for a human saccadic adaptation field such as that observed in monkeys (Noto et al., 1999). We replicate the asymmetry of the adaptation field along the horizontal meridian: saccades with a larger H-component than the 12° adapted saccade are more affected than saccades with a smaller H-component. Such horizontal asymmetry in humans was also recently reported in an investigation with four saccade targets (Alahyane et al., 2007). No asymmetry was found along the vertical meridian. Once we had described the saccadic adaptation field, we could examine the effect of adaptation on the localization of visual targets presented inside and outside the adaptation field.

In the fixation condition, we did not observe localization shifts. This was comparable to the results of the fixation condition in Awater et al. (2005). Moidell and Bedell (1988) reported a small (0.3°) but significant shift of localization in the direction of adaptation during fixation. No visual references were available during the localization judgment, and the localization shift was approximately 20% of the size of the adaptive saccade shift. In the present study, motor targeting information did not influence localization judgments. This could result from the fact that motor information was not used in the fixation condition, which would suggest that when an eye movement is prepared, supplementary mechanisms are involved in localization relative to when no movement is prepared. Alternatively, the visual reference provided by the white cross placed 12° to the right of the fixation point may have cancelled out the effect of adaptation. Further investigations are needed to clarify the effect of adaptation on localization of visual objects during fixation.

When subjects have to localize a probe appearing during the preparation of a saccade, it is important to note the different requirements of the localization task depending on the availability of post-saccadic visual references. When post-saccadic visual target information was available, exocentric (object-centered) cues could be used to localize. In this case, the post-saccadic target acted as a landmark against which other objects could be compared and realigned (Deubel, 2004). Indeed, there was a uniform shift of localization in the direction of the target shift in this condition. When the visual target was not available after the saccade, exocentric localization is no longer possible, and other sources of information must be used, such as egocentric cues. For example the motor vector of the executed saccade could be subtracted from the memorized probe position. When the executed saccade was adaptively modified, the localization of visual objects should have undergone a comparable shift and all probes should have been shifted by the amount of executed saccade adaptation. This was not the case. Rather, the localization shift was spatially non-uniform: probes closer to the fovea than the 12° saccade target were less shifted than were farther probes. This pattern of localization shifts resembled the spatial structure of the adaptation field. Indeed, the localization shift was correlated with the size of the adaptive change for saccades to the probe location. Based on this correlation, we propose that the metrics of the saccade required to acquire a target contribute to the localization of that target in space. The correlation does not imply a causal relationship, and it is also possible that the perceptual mislocalization led to the alteration of the saccade, or that both effects resulted from the common action of another mechanism. What is clear is that there is a similar effect of adaptation on both the action and perception representations of space, and that apparent localization does not depend on the sensory coordinates of the target alone.

The shift in localization of visual objects in conjunction with saccadic adaptation was also found by Bahcall and Kowler (1999) and Awater et al. (2005). Bahcall and Kowler asked subjects to judge if a probe presented after a saccade was to the left or right of the pre-saccadic target. Before adaptation, localization performance was veridical, but after adaptation the probe had to be shifted in the direction of adaptation to be perceived aligned with the pre-saccadic target. Only one probe was tested, but the amount of mislocalization was correlated with the magnitude of adaptation in both forward and backward adaptation. Awater et al. reported a significant localization shift in the direction of adaptation when probes were flashed more than 100 ms before the saccade. The authors did not compare the amount of localization shift to the amount of adaptation, but noted that similarly to the present results, the mislocalization was restricted to probes close to the saccade endpoint. Recent evidence suggests that saccadic adaptation might also be accompanied by a congruent shift of pointing judgments (MC Morrone, personal communication).

The results show that saccadic adaptation modifies the apparent spatial localization of visual objects according to the position of that object relative to the adaptation field: when the metrics of a saccade are adaptively modified, there is a concomitant modification of apparent space. The representation of an object's visual location depends, at least in part, on motor information about the movement that would be needed to acquire it, suggesting that our perception depends, at least in part, on our potential to act.

4. Experimental procedure

4.1. *Subjects*

Four subjects (two authors and two naive observers) with normal vision participated in the experiment. All were familiar with eye movement recording and gave their informed consent in accordance with the Declaration of Helsinki (2004).

4.2. *Instruments*

Subjects sat in a dimly lit room and stimuli were presented on an Iiyama monitor (HM240DT) with a refresh rate of 200 Hz. Subjects were seated 45 cm from the screen such that it subtended 51° by 39° of visual angle. Eye movements were monitored by an Eye Link II (SR Research Ltd., Osgoode, Ontario, Canada) and sampled at 250 Hz. The eye tracker is head-mounted and the head was further stabilized by a chin rest. The absolute spatial resolution of the tracker is $<0.5°$. Saccades were detected by velocity ($>22°/s$) and acceleration ($>4000°/s$) thresholds. The delay between saccade onset and the generation of a new image on the computer screen took approximately 28 ms. At an average saccade duration of 45 ms, this was sufficient for intra-saccadic stimulus changes. Before each session, the tracker was calibrated by having the subject fixate nine positions on the screen. Before each experimental trial, a drift correction was performed that matched the gaze position during initial fixation to the coordinates of the fixation point.

4.3. *Stimuli*

Stimuli consisted of $1°\times1°$ crosses (black, 0.1 cd/m^2, or white, 13 cd/m^2, fixation cross and white saccade targets) and white $1\times1°$ squares (localization probes, 28 cd/m^2) on a medium gray background (0.2 cd/m^2). The fixation cross was located about 12° from the left border of the screen and equidistantly from the top and bottom. Its coordinates were fixed by convention at (0°, 0°), and was either white or black, indicating that subjects had to make a saccade or hold fixation in a particular trial. Saccade target position and probe position were chosen pseudo-randomly from an array of 39 tested positions (see Conditions).

4.4. *Procedure*

A trial began with the presentation of the fixation cross. When subjects had established fixation they pressed a button to begin the trial. The button press started the automatic drift correction at the fixation cross position, and subsequently the presentation of a saccade target. When a saccade was required, the fixation cross disappeared after a variable delay (600–800 ms), and this was the go-signal for the saccade. 40 to

80 ms later, a probe appeared for two video frames (≈10 ms). Subjects made their saccade and depending on condition and phase, the saccade target was maintained, extinguished or stepped back during the saccade (see next section). Subjects were asked to maintain fixation at the new eye position until the appearance of the mouse pointer at a random location 500 ms after saccade detection, and then to use the mouse pointer to click on the position they thought the probe had appeared in (Fig. 4a). During this time, they were free to move their eyes and the response was not under any time pressure. Once they had given their response, the fixation cross for the next trial was presented. When the fixation cross was black, subjects were to maintain fixation. In such fixation trials, the fixation cross did not disappear and all other events occurred after delays comparable to the trials in which saccades were required, except that the saccade target was never stepped back but remained visible until the end of the trial (including the response period). The mouse was placed to the right of the computer and subjects used their right hand to respond.

The timing of the probe was designed to have it appear more than 100 ms before saccade onset. This delay is important to take into account in the localization of briefly flashed objects, as localization is compressed towards the saccade target about 50 ms before saccade onset (Ross et al., 1997; Lappe et al., 2000). Furthermore, when the upcoming saccade is adapted, the compression is centered on the adapted endpoint (Awater et al., 2005). We wanted to test localization of probes before any such peri-saccadic mislocalizations came into play. Therefore, we selected a stimulus onset asynchrony (SOA) between the go-signal and probe presentation such that probe onset occurred more than 100 ms before saccade onset. Based on saccade latencies measured in pre-tests (around 200 ms), this SOA was fixed at 40–80 ms. In the course of the experiment, subjects sometimes made fast latency saccades causing probe presentation to occur less than 100 ms before the saccade (27%). These trials were discarded, and the average time between probe presentation and saccade onset was 157±31 ms, with no effect of phase ($F<1$) nor condition ($F<1$).

4.5. Conditions

Four conditions were tested across two experimental phases, pre-adaptation and adaptation.

4.5.1. *Saccadic adaptation and transfer*

Saccadic adaptation was evoked for 12° rightward saccades. In the adaptation phase, during the saccade, the saccade target stepped back by 4°. Transfer of the 12° horizontal saccade adaptation to 38 different saccades was tested. The saccade target was extinguished during these saccades in order to prevent visual feedback from interfering with the adaptation of the 12° horizontal saccade. The following positions were tested:

(a) six positions with the same horizontal (H-) component as the adapted saccade (+12°) but with a different vertical (V-) component (2°, 4°, 8° both above and below);
(b) eight positions with the same V-component as the adapted saccade (0°) but with a different H-component (4°, 6°, 8°, 10°, 14,° 16°, 20, 24°);
(c) six positions with the same amplitude (12°) but a different direction (33°, 57°, 90° both clockwise and counterclockwise);
(d) nineteen positions with different H-components, V-components, amplitudes and direction as the adapted saccade.

The spatial layout of the tested positions can be seen in Figs. 2a and 3.

4.5.2. *Probe localization judgments*

Three conditions examined localization performance. In all three, the saccade target was always located 12° to the right of the fixation point, and 39 probe positions were tested. These positions were the same as those used to evoke saccades in the saccade condition (see Figs. 2a, 3). In one condition, the saccade target was extinguished during the saccade. Therefore, when the saccade landed, no visual stimuli were present on the screen, and subjects performed the subsequent localization judgment without post-saccadic visual references. In another condition, the saccade target remained on during the saccade and during the response period. When the saccade landed, subjects performed the localization judgment with a visual reference. In the third condition in which localization was tested, subjects had to maintain fixation until the presentation of the mouse pointer. Both the fixation cross and the white cross 12° to the right were visible until the end of the trial (including the response period). All other events occurred after delays comparable to the two other localization conditions (see Fig. 1a).

In each session, the four conditions were mixed and tested in both pre-adaptation and adaptation phases. In the pre-adaptation phase (100 trials), 66% of trials required the subject to make a saccade towards the target presented 12° to the right. In half of these, the subject then performed a localization judgment without visual references, and with visual references in the other half. Subjects had to maintain fixation in 17% of trials. In the remaining 17%, the saccade target could be any of the 39 possible positions. The adaptation phase consisted in 150 trials. In the first 50, subjects made a saccade towards the target presented at (12°, 0°) and the target was stepped back to (8°, 0°) to evoke saccadic adaptation. A probe appeared at one of the 39 tested positions. The 100 final trials were identical to the pre-adaptation phase, with the important exception that in trials where the saccade target 12° to the right remained visible throughout the trial, it was stepped back during the saccade to (8°, 0°) to maintain adaptation. Averages from the pre-adaptation phase take all 100 trials of this phase into account. Averages from the adaptation phase take the final 100 trials into account.

Subjects took 11–14 sessions which lasted approximately 1 h each. When two sessions were separated by less than 48 h, the second was preceded by 25 pre-adaptation trials with the saccade target 12° to the right to ensure that there was no retention of adaptation from the previous day's session.

4.6. Data analysis

Trials on which blinks or saccade endpoints more than ±2 SD from the individual mean occurred (<1%), trials on which the estimated probe position was more than ±2 SD from the individual mean (<2%), and trials in the fixation condition during which subjects broke fixation (43% of the fixation trials) were eliminated from the analyses.

After elimination, for each of the four subjects, each tested position in each phase had on average 34±6 localization estimates with post-saccadic visual references, 7±2 localization estimates without post-saccadic visual references, 9±2 localization estimates during fixation, and 7±2 saccades towards it. We ran analyses of variance (ANOVA) on these data. For analyses run on saccade latency, time between probe presentation and saccade onset, and saccade amplitude, a 2×2 factorial design was adopted. Factors were Phase (pre-adaptation/adaptation) and Condition (Localization with visual references/Localization without visual references/Saccade). In the one-way analysis (%adaptation), only Condition was tested as a factor. *p* Values are given in parentheses. When indicated, Student's *t*-tests were also performed.

Acknowledgments

T.C. was supported by a travel grant from Boeringer Ingelheim Fonds. M.L. is supported by the German Science Foundation DFG LA-952/2 and LA-952/3, the German Ministry of Education and Research project Visuo-spatial Cognition, and the EC Project Drivsco.

REFERENCES

Abel, L., Schmidt, D., Dell'Osso, L., Daroff, R., 1978. Saccadic system plasticity in humans. Ann. Neurol. 4, 313–318.

Alahyane, N., Salemme, R., Urquizar, C., Cotti, J., Guillaume, A., Vercher, J.-L., Pélisson, D., 2007. Oculomotor plastiticy: are mechanisms of adaptation for reactive and voluntary saccades separate? Brain Res. 135, 107–121.

Awater, H., Burr, D., Lappe, M., Morrone, M.C., Goldberg, M., 2005. The effect of saccadic adaptation on localization of visual targets. J. Neurophysiol. 93, 3605–3614.

Bahcall, D., Kowler, E., 1999. Illusory shifts in visual direction accompany adaptation of saccadic eye movements. Nature 26, 864–866.

Bridgeman, B., Hendry, D., Stark, L., 1975. Failure to detect displacement of the visual world during saccadic eye movements. Vis. Res. 15, 719–722.

Collins, T., Doré-Mazars, K., 2006. Eye movement signals influence perception, evidence from the adaptation of reactive and volitional saccades. Vis. Res. 46, 3659–3673.

Deubel, H., 1995. Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. Vis. Res. 35, 3529–3540.

Deubel, H., 2004. Localization of targets across saccades, Role of landmark objects. Vis. Cogn. 11, 173–202.

Deubel, H., Wolf, W., Hauske, G., 1986. Adaptive gain control of saccadic eye movements. Hum. Neurobiol. 5, 245–253.

Deubel, H., Schnieder, W., Bridgeman, B., 1996. Postsaccadic target blanking prevents saccadic suppression of image displacement. Vis. Res. 36, 985–996.

Deubel, H., Bridgeman, B., Schneider, W., 1998. Immediate post-saccadic information mediates space constancy. Vis. Res. 38, 3147–3159.

Frens, M., van Opstal, A., 1994. Transfer of short-term adaptation in saccadic eye movements. Exp. Brain. Res. 100, 293–306.

Fuchs, A.F., Reiner, D., Pong, M., 1996. Transfer of gain changes from targeting to other types of saccade in the monkey, constraints on possible sites of saccadic gain adaptation. J. Neurophysiol. 76, 2522–2535.

Lappe, M., Awater, H., Krekelberg, B., 2000. Postsaccadic visual references generate presaccadic compression of space. Nature 403, 892–895.

McLaughlin, S., 1967. Parametric adjustment in saccadic eye movements. Percept. Psychophys. 2, 359–362.

Moidell, B., Bedell, H., 1988. Changes in oculocentric visual direction induced by the recalibration of saccades. Vis. Res. 28, 329–336.

Noto, C., Watanabe, S., Fuchs, A.F., 1999. Characteristics of simian adaptation fields produced by behavioral changes in saccade size and direction. J. Neurophysiol. 81, 2798–2813.

Optican, L., Robinson, D., 1980. Cerebellar-dependent adaptive control of primate saccadic system. J. Neurophysiol. 44, 1058–1076.

Ross, J., Morrone, M.C., Burr, D., 1997. Compression of visual space before saccades. Nature 386, 598–601.

World Medical Association Declaration of Helsinki, 2004.