Visual versus motor vector inversions in the antisaccade task: A behavioral investigation with saccadic adaptation.

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Abstract

In the antisaccade task, subjects must execute an eye movement away from a visual target. Correctly executing an antisaccade requires inhibiting a prosaccade towards the visual target and programming a movement to the opposite side. This movement could be based on the inversion of the visual vector, corresponding to the distance between the fixation point and the visual target, or the motor vector of the unwanted prosaccade. We dissociated the two vectors by means of saccadic adaptation. Adaptation can be observed when systematic targeting errors are caused by the displacement of the visual target during the saccade. Adaptation progressively modifies saccade amplitude (defined by the motor vector) such that it becomes appropriate to the post-saccadic stimulus position, and thus different from the visual vector of the target. If antisaccade preparation depended on visual vector inversion, then rightward prosaccade adaptation should not transfer to leftward antisaccades (which are based on the same visual vector) but should transfer to rightward antisaccades (which are based on the same, adapted motor vector). If antisaccade preparation depended on motor vector inversion, then rightward prosaccade adaptation should transfer to leftward antisaccades (which are based on the same, adapted motor vector) but should not transfer to rightward antisaccades (which are based on a non-adapted motor vector). The results are in line with the first hypothesis, showing that vector inversion precedes saccadic adaptation and suggesting that antisaccade preparation depends on the inversion of the visual target vector.
INTRODUCTION

Moving the eyes toward a visual target is a sensory-motor task in which both the input (the target) and the output (the eye movement) are clearly defined. Visual and motor processes are usually in spatial alignment, but they can be dissociated experimentally in the antisaccade task, in which an eye movement away from a visual target must be made (see Munoz and Everling, 2004 for a review). Programming an antisaccade is generally assumed to take two steps: first the inhibition of the saccade toward the visual target (prosaccade) and then the programming of a saccade to the opposite direction (antisaccade). Indeed, antisaccade latency is longer than prosaccades because of these supplementary processes. The process by which the location of the visual stimulus is transformed into a motor command to the opposite side could take two forms. The visual vector – corresponding to the distance between central gaze and the visual target – could be inverted. Visual vector inversion would thus require computing the position of the visual target, reflecting that about the origin, and then programming a saccade to it. Alternatively, the motor vector – corresponding to the motor command of the inhibited prosaccade – could be inverted. Motor vector inversion would require computing the metrics of the prosaccade directed towards the visual stimulus, then reflecting the spatial attributes of the motor plan about the origin.

Evidence for vector inversion in the antisaccade task was reported in the frontal eye fields (FEF) by Sato and Schall (2003; Schall, 2004). (Because the FEF movement neurons represent the veridical saccade, the command to invert the vector must be at or upstream of the FEF). In prosaccade trials, FEF visual neurons were activated when the target was inside but not when it was outside their receptive field. In antisaccade trials, the same neurons were initially responsive to the target but then switched their activity and responded more to the target placed on the opposite side, outside their receptive field, but towards which the upcoming antisaccade would be directed. This suggests that at some point during the delay between target presentation and movement onset, there is a switch in activity. However, whether this activity was motor or visual remained unanswered. Further evidence for vector inversion was found in the lateral intraparietal area (LIP) by Zhang and Barash (2000; 2004). LIP visual neurons respond to the visual target regardless of the direction of the upcoming saccade. A subset (30%) of these visual neurons also shows ‘paradoxical’ activity: in addition to the visual response to targets inside the receptive field, when the upcoming antisaccade was directed towards the receptive field, these neurons also had a visual response to the target on the opposite side of their receptive field (see also Gottlieb et al. 2005). Zhang and Barash (2000; 2004) proposed that this paradoxical activity could be related to the inversion of the visual vector (see also Barash, 2003; Barash and Zhang, 2006). Funahashi et al. (1993) reported ‘paradoxical’ activity in prefrontal motor neurons that were activated when an antisaccade was made in the direction opposite their movement field. Medendorp et al. (2005) demonstrated that goal-related activity in the putative human homologue of monkey LIP in the posterior parietal cortex (PPC) switched from the contralateral to the ipsilateral PPC, suggesting that the visual stimulus location was remapped to the opposite side. Nyffeler et al. (2007) recently reported a case study of selective deficit in the antisaccade task following PPC damage. Ipsilateral prosaccades were normometric but both contralateral prosaccades
and ipsilateral antisaccades were hypometric. This pattern could result from a deficit in the contralateral visual vector due to the parietal damage, and is consistent with the inversion of a (damaged) visual vector during antisaccade programming.

We sought to investigate vector inversion in antisaccades in humans with a behavioral approach: saccadic adaptation. Saccadic adaptation occurs following targeting errors, such as those observed after extraocular muscle dysfunction (Abel et al. 1978) or in the laboratory with the double-step procedure (McLaughlin 1967): the visual target is surreptitiously displaced during the saccade directed toward it, thus mimicking a targeting error when the eye lands. After several such trials, saccade amplitude adapts to compensate for the artificial error, thus introducing a discrepancy between the visual vector and the motor vector (see Hopp and Fuchs, 2004 for a review). Indeed, saccadic adaptation affects the motor vector of the saccade and not the visual vector of the target. This has been supported by several lines of evidence. First, saccades of a given vector directed towards different positions of the visual field were measured before and after the adaptation of a vector of same magnitude and direction but aiming for a different position. If adaptation led to a local modification of the representation of the visual field, then the tested saccades should not be affected by the adaptation. Several studies have shown that this is not the case (Wallman and Fuchs, 1998; Frens and van Opstal, 1994; Albano, 1996). A second approach examined the effect of adaptation on non-visually-guided saccades. If adaptation modifies the representation of the visual field, then the adaptation of a given saccade vector should not transfer to saccades with the same vector but directed to an auditory stimulus. Frens and van Opstal (1994) showed on the contrary that adaptation of visually-guided saccades transferred to auditorily-guided saccades. A third approach examined the transfer of adaptation to manual movements. If saccadic adaptation modified the representation of visual space, then all movements guided in this space should be modified by adaptation transfer. On the contrary, several studies have shown no transfer of saccadic adaptation to movements of the head (Kröller et al. 1999) or the hand (McLauglin et al. 1968; but see de Graaf et al. 1995 for limited transfer).

The goal of our study was to examine how the adaptation of a saccadic motor vector transfers to antisaccades. To test this issue optimally, we adapted volitional rather than reactive prosaccades because adaptation transfer is usually found within a saccade category (i.e. volitional or reactive) but not systematically between saccade categories (i.e. reactive to volitional; we would thus not expect any transfer from reactive prosaccades to antisaccades in any direction – see Methods). In the first experiment, we adapted a horizontal rightward prosaccade and tested the transfer of this adaptation to leftward and rightward anti- and prosaccades of similar amplitude. The four saccade types examined are illustrated in Figure 1.

Insert Figure 1 here

We expected rightward prosaccade adaptation not to transfer to leftward prosaccades because adaptation in one direction does not transfer to saccades in the other direction (Semmlow et al. 1989). Two hypotheses can be made about the transfer of rightward prosaccade adaptation (V+M+) to antisaccades. We distinguished the motor vector inversion hypothesis from the visual vector inversion hypothesis (Figure 1). If antisaccades depend on the inversion of the motor vector of the unexecuted
prosaccade, then adaptation should transfer to antisaccades to the opposite location (V+M-). Prosaccade adaptation should not transfer to antisaccades made in the same direction (V-M+) because these antisaccades would be based on the motor vector of the unexecuted prosaccade in the opposite direction, which was not adapted. This hypothesis assumes that motor vector inversion occurs after saccadic adaptation. Alternatively, if antisaccades depend on the inversion of the visual vector, then prosaccade adaptation should transfer to antisaccades in the same direction (V-M+), because the visual vector of the target on the opposite side would first be inverted and then the saccade programmed. This saccade would thereafter be based on the same sensory-motor transformation as the adapted saccade and should be adapted. Rightward prosaccade adaptation should not transfer to antisaccades in the opposite direction (V+M-) because their visual vector is not influenced by the prosaccade adaptation. This hypothesis assumes that visual vector inversion occurs before saccadic adaptation.

These alternative hypotheses rest on two related assumptions. First, that saccadic adaptation modifies the motor vector. Consequently, if antisaccades depend on the inversion of the visual vector, they would not be affected by adaptation. Second, that the motor vector is affected by adaptation before vector inversion. Consequently, if antisaccades depend on the inversion of the motor vector, they would be affected by adaptation. We return to two assumptions in the General Discussion.

In the first experiment, there were only two possible targets (left and right). In the second experiment, the number of saccade targets was increased to six possible saccade targets, only one of which was adapted. Moreover, we tested both rightward and leftward prosaccade adaptation. Both experiments led to similar results.

EXPERIMENT 1

METHODS

Subjects

Seven subjects with normal vision participated in this experiment. Four were naïve to the goal of the experiment and three were authors (S1, S3, S6). All were familiar with the eye movement recording and gave their informed consent. The experimental protocol was approved by the local ethics committee as being within the regulations for human experimentation under the Helsinki protocol.

Instruments and eye movement recording

The experimental sessions took place in a dimly lit room. Subjects were seated 57 cm away from the screen and their head kept stable with a submaxillar dental print and forehead rest. The stimuli were presented on Iiyama HM240DT monitor with a refresh rate of 170 Hz. Eye movements were monitored by a Bouis Oculomotor system (Bach, Bouis and Fischer, 1983), with an absolute resolution of 6 arc minutes and a linear output over 12 degrees of visual angle. Viewing was binocular but only the movements of the right eye were monitored. Signal from the oculometer was sampled every 2 ms. Saccades were detected with an in-house program using Labview 7.1 by velocity (>40°/sec), acceleration (>3000°/sec/sec) and minimal displacement (0.15°) thresholds.
Stimuli and procedure

Stimuli were 1°x1° white crosses on a medium gray background. The fixation cross was positioned in the center of the screen and the saccade target could appear 6° to the left or right.

Each session began with a full calibration procedure during which subjects had to saccade to 5 bars presented successively from left to right in steps of 3°. Reference measures were taken for each of the five bars. If the variability of each measure was below a threshold (0.4 volts), and if the values for the five bars were linear, the calibration was considered successful and the experiment started. Each experimental trial started with a calibration check. Subjects were required to fixate a bar that appeared in the center of the screen. If the recorded value was different from full calibration (±0.1°), it was automatically renewed. When successful calibration was detected, the fixation cross and saccade target appeared simultaneously. After 600 ms, the fixation cross disappeared, this was the go-signal for the saccade. After their saccade, subjects had to press on a button to initiate the next trial.

Each session was composed of 320 trials in three successive phases: pre-test, adaptation and post-test. In the pre-test phase, subjects performed a block of 40 antisaccade trials and then a block of 40 prosaccade trials. The instructions were given to the subject before each block on the screen, but no feedback as to their saccade performance was ever given. In antisaccade trials, subjects were instructed to look to the mirror position. In each of the pre-test blocks, the target appeared equally often on the left or right. During the saccade directed toward it, the target disappeared and the screen remained blank until the subject pressed a button to indicate she was ready for the next trial. The two pre-test blocks were followed by the adaptation phase. Subjects were instructed to make only prosaccades. The saccade target appeared to the right in 100 trials (62.5%). During the rightward saccade, the target stepped back by 2°. In the remaining 60 trials, the saccade target appeared to the left and did not step back during the saccade. All trials were randomly mixed. Finally, the adaptation phase was followed by a post-test phase in which 40 prosaccade then 40 antisaccade trials were tested in separate blocks. The characteristics of these two blocks were identical to the pre-test. In particular, the target was extinguished during the saccade directed towards it, such that when the eyes landed there was no longer a visual reference from which a targeting error signal could be computed (Seeberger et al. 2002). This allowed adaptation to be maintained throughout the 80 post-test trials. Five subjects took two replications of the 320-trial session (separated by a minimum of 48 hours), and two subjects took one replication. We averaged across the two replications and compared the mean results of seven subjects.

By using a 600ms overlap between the fixation cross and the saccade target, we elicited volitional saccades. We tested volitional rather than reactive prosaccades because reactive saccade adaptation does not transfer to volitional saccades (Deubel, 1995; Collins and Doré-Mazars, 2006; Alahyane et al. 2007). Although transfer of adaptation from visually-guided volitional saccades to antisaccades has not been specifically tested, robust transfer from one type of volitional saccade to another has been reported (Deubel, 1995; Fujita et al. 2002).

We tested only backward adaptation by stepping the visual target in the direction opposite the saccade during its execution, and did not test forward adaptation (during which the target steps in the same direction as the saccade and leads to an increase of amplitude). Backward adaptation has been
shown to be faster than forward adaptation (Bahcall & Kowler, 2000). Because we wanted to obtain optimal amounts of adaptation in order to be able to examine transfer, we chose to study backward adaptation only.

**Data analyses**

We analyzed primary saccades. The following trials were eliminated from further analyses: prosaccade errors in antisaccade trials (1%), antisaccade errors in prosaccade trials (1%), trials in which blinks (2%) or anticipatory saccades (3%; saccade onset before the go-signal or with latency <100 ms) occurred.

Percent gain change was calculated as the ratio of the difference between the mean gain (saccade amplitude / target eccentricity) of each saccade type and each direction in the pre-test phase (n=20) and the mean gain of the same saccade type and direction in the post-test phase (n=20) to the pre-test gain:

\[
\text{% gain change} = ((\text{pre-test gain} - \text{post-test gain}) / \text{pre-test gain}) \times 100
\]

The % gain change for rightward prosaccades (% gain change\(_{V+M+}\)) was taken as the indicator of the amount of saccadic adaptation:

\[
\text{Amount of adaptation} = ((\text{pre-test gain}_{V+M+} - \text{post-test gain}_{V+M+}) / \text{pre-test gain}_{V+M+}) \times 100
\]

Adaptation transfer was calculated by comparing the mean % gain change for each of the tested saccades to the amount of adaptation:

\[
\text{% adaptation transfer} = \text{% gain change}_{\text{tested saccade}} / \text{% gain change}_{V+M+}
\]

We ran a 4 (Saccade type: V+M+, V+M-, V-M+, V-M-) x 2 (Phase: Pre- versus Post-test) ANOVA on saccade gain and latency. A 2 (Target side: Left versus Right) x 2 (Saccade: Pro- versus anti-) ANOVA was run on adaptation transfer. P-values are indicated in parentheses. When indicated, T-tests were also performed.

**RESULTS**

**Baseline characteristics**

In the pre-test phase, mean gain of all prosaccades (rightward and leftward) was 0.92±0.10, and mean gain of all antisaccades was 0.87±0.24 (mean ± standard deviation). Mean saccade latency (time between the go-signal – fixation offset – and saccade onset) was significantly different between pro- and antisaccades: 182±26 ms versus 259±60 ms respectively (F(3,9)=4.2, p<.04), but did not depend on phase (F<1). Figure 2 presents the mean data for gain and latency.

Insert Figure 2 here

**Rightward prosaccade adaptation**

In the pre-test phase, the mean gain of rightward prosaccades was 0.96±0.12. After 100 trials in which the target was stepped back during the saccade (i.e. in the post-test), mean saccade gain decreased significantly to 0.80±0.11 (F(1,3)=73.3, p<.0006). As can be seen in the individual time course in Figure 3, the adaptive reduction in gain reduction was progressive. The mean amount of adaptation was 16±2%.  

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**Adaptation transfer**

Figure 4 shows the % transfer of adaptation for all four tested saccade types. The top panel describes the average data. The standard deviation is approximately 30 percentage points; as shown in the individual subject data in the bottom panels of Figure 4, while the values of the adaptation transfer differed between subjects, the pattern of results was quite similar across subjects.

Neither saccade type nor target side affected % transfer, but the interaction between the two was significant ($F(1,3)=49.3, p<.003$). This interaction revealed that for prosaccades, adaptation transfer was found for saccades directed to the right target (V+M+) but not for saccades directed to the left (V-M-), whereas for antisaccades, the reverse was true: adaptation transferred to saccades evoked by the left target (rightward antisaccades, V-M+) but not to those evoked by the right target (leftward antisaccades, V+M-). Indeed, rightward prosaccade adaptation transferred fully to rightward antisaccades (100±33% transfer, not significantly different from 100, Student t-test, $p>0.9$) but not to leftward antisaccades (4±31% transfer, not significantly different from 0, Student t-test, $p>0.7$). As expected, rightward prosaccade adaptation did not transfer to leftward prosaccades (-8±31% transfer, not significantly different from 0, Student t-test, $p>0.5$).

**DISCUSSION**

We adapted a rightward prosaccade and tested the transfer to pro- and antisaccades in the same or opposite direction. The goal was to distinguish between hypotheses regarding the type of vector inversion that must be made during the programming of an antisaccade.

We did not observe any transfer of rightward prosaccade adaptation to leftward prosaccades, as expected because they are outside the adaptation field, i.e. the spatial zone around the adapted saccade vector inside which adaptation transfers to other vectors (Semmlow et al. 1989; Noto et al., 1999; Collins et al., 2007). Of interest was the transfer of adaptation to antisaccades. We hypothesized that if antisaccades depended on the inversion of the motor vector of the prosaccade, then rightward prosaccade adaptation should have transferred to the leftward antisaccade, because such saccades would depend on the inversion of an adapted vector. Furthermore, as rightward antisaccades would depend on the inversion of the leftward prosaccade vector which should not be affected by saccadic adaptation because it is outside the adaptation field, the gain of rightward antisaccades should not be modified after adaptation. Neither of these hypotheses was verified, going against the motor vector inversion hypothesis. We observed no transfer of adaptation to leftward antisaccades but a complete transfer of adaptation to rightward antisaccades. Such results are in line with the visual vector inversion hypothesis. Indeed, the visual vector of rightward antisaccades depends on the lefthand visual target. This vector is inverted and then the motor vector would be prepared. Therefore, the sensory-motor transformation takes place on the adapted side, which can explain why adaptation transferred to rightward antisaccades.
Our subjects were required to make a prosaccade or antisaccade to one of two possible targets. Because of the relative simplicity of the spatial computations necessary to perform this task, it is possible that subjects simply prepared two saccade programs and executed whichever one was required on a given trial. In this case, a vector inversion could take place only on the first trial or trials. Although the latency of antisaccades was longer than that of prosaccades throughout all phases of the experiment, possibly due to greater spatial computation needs, we wanted to make sure to eliminate this possibility in a task where the need for spatial computation on every trial was more explicit. We did this in Experiment 2 by increasing the number of possible saccade targets from two to six. We also repeated the experiment with leftward adaptation.

EXPERIMENT 2
METHODS
Subjects

Five subjects participated in the experiment; two were authors (S1, S3) and four had also participated in the previous experiment (S1-4).

Instruments and eye movement recording
The instruments and recording were identical to Experiment 1.

Stimuli and procedure
The stimuli and calibration procedure were identical to Experiment 1.

Each subject ran two sessions on different days (separated by a minimum of 48 hours), a rightward adaptation session and a leftward adaptation session. Each session was composed of three successive phases: pre-test (124 trials), adaptation (180 trials) and post-test (124 trials). The pre-test was broken into two successive blocks of 62 antisaccade trials and then 62 prosaccade trials. In each block, the saccade target was located at one of six locations: -8°, -6°, -4°, +4°, +6°, +8° from screen center where the fixation cross was located. Targets at -6° and +6° were tested 15 times, the others were tested 8 times. During the saccade, the target was extinguished and the screen remained blank until the subject pressed a button to initiate the next trial. In the pre-test and post-test phases, the six target positions were mixed. In the adaptation phase (180 trials) subjects were instructed to make only prosaccades. Four saccade targets were mixed. In the rightward adaptation session, we tested one target 6° to the right (120 trials) and three targets to the left (20 trials each) (-8°, -6°, -4°). During the saccade directed towards the target located at +6°, it was stepped back by 2° and remained there until the end of the trial. The three lefthand targets were not stepped back during the saccades directed to them but remained on until the end of the trial. In the leftward adaptation session, we tested one target 6° to the left (120 trials) and three to the right (20 trials each) (+4°, +6°, +8°). The intra-saccadic target back-step occurred only during the saccade directed to the target at -6°. For both adaptation sessions, the post-test was identical to the pre-test except that the 62 prosaccades were run first.
As in the previous experiment, the go-signal to make the saccade was always the extinction of the central fixation cross, 600 ms after the target presentation: we thus evoked volitional prosaccades. Each subject took one replication of the rightward adaptation session and one replication of the leftward adaptation session. Three of them began with the rightward adaptation session and two with the leftward adaptation session.

**Data analyses**

We analyzed primary saccades. The following trials were eliminated from further analyses: prosaccade errors in antisaccade trials (1%), antisaccade errors in prosaccade trials (<1%), trials in which blinks or anticipatory saccades (10%; saccade onset before the go-signal or with latency <100 ms) occurred.

Percent gain change, amount of adaptation and % transfer were calculated for each of the six saccade targets as before. We ran a 3 (Saccade eccentricity: 8°, 6°, 4°) x 2 (Phase: Pre- versus Post-test) x 2 (Saccade Direction: left versus rightward saccades) x 2 (Adaptation Side: left versus right adaptation) ANOVA on saccade gain and latency; each session (leftward versus rightward adaptation) was analyzed separately. A 2 (Target side: Left versus Right) x 3 (Eccentricity: 8°, 6°, 4°) x 2 (Saccade: Pro- versus anti-) x 2 (Adaptation Side: left versus right adaptation) ANOVA was run on adaptation transfer. When indicated, T-tests were also performed.

**RESULTS**

**Baseline characteristics**

In the pre-test phase, the mean gain of all prosaccades was 0.89±0.06, and mean gain of all antisaccades was 0.90±0.19. Antisaccade latency was longer than prosaccade latency (259±41 ms versus 198±35 ms; F(1,4)=22.3, p<.01) but depended neither on phase (F(1,4)=3.4, p>.1) nor saccade target position (F<1). Figure 5 presents the mean gain and latency for all conditions.

Insert Figure 5 here

**Prosaccade adaptation**

In the leftward adaptation session, the mean pre-test gain of leftward 6° prosaccades was 0.87±0.09. The mean post-test gain was significantly decreased to 0.73±0.07 (F). The amount of adaptation was 23±4%. Figure 6 presents an individual time course of adaptation. We present saccade endpoint rather than saccade gain (as in the time course presented in Figure 2) so that the different target eccentricities can be distinguished. Adaptation occurred progressively.

Insert Figure 6 here

In the rightward adaptation session, the mean pre-test gain of rightward 6° prosaccades was 0.95±0.07. The mean post-test gain of 0.77±0.06 differed significantly from the pre-test (F(1,4)=69.9, p<.002)). The amount of adaptation was 18±5%. The amount of adaptation did not differ between left and rightward adaptation sessions (F(1,4)=4.5, p>.1).

**Adaptation transfer**
Figure 7 presents percent adaptation transfer for the tested saccade types, depending on the direction of adaptation (left or right). As in Experiment 1, between-subject variability was relatively large, nevertheless the pattern of results was similar across subjects, as can be seen in Figure 7 and indicated by the statistical analyses below.

Globally, there was no effect of adaptation side (leftward versus rightward adaptation; F<1), but the triple interaction between saccade type (pro- versus antisaccades), direction (left versus rightward saccades) and adaptation side was significant (F(1,4)=447.0, p<.0001). This interaction reveals that leftward adaptation transferred to leftward but not rightward prosaccades, and to leftward but not rightward antisaccades (Figure 7A). The transfer of leftward prosaccade adaptation to leftward antisaccades evoked by the 6° target was not significantly different from 100% (Student t-test, p<.03). Transfer to both rightward saccades (both pro and anti) was not significantly different from 0% (Student t-tests, ps>0.2). For rightward adaptation, the reverse was observed: rightward prosaccade adaptation transferred to rightward but not leftward prosaccades in the post-test, and to rightward but not leftward antisaccades (Figure 7B). Student t-tests revealed that the transfer of rightward prosaccade adaptation to rightward antisaccades evoked by the 6° target was significantly different from both 0% (p<.01) and 100% (p<.01); the 95% confidence interval was 19-70%. Transfer to both leftward pro and antisaccades was not significantly different from 0% (Student t-tests, ps>0.3).

There was no overall effect of target eccentricity (F(2,8)=2.7, p>.12). Descriptively, it appears that the transfer of adaptation from saccades aiming for a 6° target to saccades aiming for 4° or 8° targets is less than 100%. However, probably due to the inter-subject variability, these differences did not reach significance.

DISCUSSION

The results of the second experiment confirm and extend those of the first experiment. Rightward prosaccade adaptation transferred to antisaccades in the same direction (evoked by a visual target on the opposite side) but not to antisaccades directed in the opposite direction (evoked by the same visual target). As in the previous experiment, these results are compatible with the idea that the visual vector rather than the motor vector is inverted during antisaccade preparation. This second experiment replicated this result with leftward prosaccade adaptation.

GENERAL DISCUSSION

The goal of the two experiments presented here was to distinguish between two alternative hypotheses regarding the type of vector inversion made during the programming of an antisaccade. Antisaccade preparation could involve the inversion of the visual vector of the stimulus in response to which a saccade is made, or alternatively could involve the inversion of the motor vector of the unwanted prosaccade to the visual stimulus. We dissociated these two vectors by means of saccadic adaptation which modifies the motor vector but does not affect the visual vector. In the first experiment, we adapted a rightward volitional prosaccade and tested the transfer to pro- and
antisaccades in the same or opposite direction. The results showed that adaptation transferred to antisaccades in the same but not in the opposite direction.

In the second experiment, we replicated the first experiment with both leftward and rightward volitional prosaccade adaptation. We also increased the number of possible saccade targets to increase the spatial computation load and ensure that a vector inversion was necessary on a trial-by-trial basis. This second experiment confirmed the results of the first experiment: prosaccade adaptation transferred to antisaccades in the same direction (evoked by a visual stimulus in the opposite hemifield) but not to antisaccades in the opposite direction (evoked by a visual stimulus in the adapted hemifield).

Overall, these results are compatible with the predictions of the visual vector inversion hypothesis. Recall that such a hypothesis depends on the assumption that saccadic adaptation is motor rather visual (see Introduction). Our results are also consistent with this view: if adaptation resulted from a modification of the sensory coordinates of the target, then the visual vector would have been affected and when it was inverted during antisaccade preparation, we should have observed transfer. This was clearly not the case, providing evidence against sensory adaptation and in favor of motor adaptation. This result also suggests that the neural site of saccadic adaptation is not in the parietal cortex where the visual vector inversion likely takes place. We propose that during antisaccade preparation, the visual vector is inverted and the resulting motor vector is adapted by transfer if it is inside the adaptation field of the adapted prosaccade. The results do not fit with the hypothesis that the inverted vector is motor. Indeed, if a motor vector is the final outcome of sensory-motor transformation, it should be adapted before the inversion and we should have observed a different pattern of results (Figure 1, motor vector inversion hypothesis).

However, our results are compatible with an alternative interpretation according to which during antisaccade preparation, the motor vector could be inverted before the level of adaptation and subsequently modified. We call this the “early motor vector” hypothesis as opposed to the “final motor vector” hypothesis. According to the “early motor vector” hypothesis, after rightward prosaccade adaptation, rightward antisaccades would depend on the inversion of an unadapted leftward motor vector which would be adapted after having been inverted to the right side. No transfer to the opposite (leftward) antisaccade would be expected. In this case, the absence of transfer we observed would not reflect visual vector inversion but the inversion of an early motor vector.

Our results alone cannot definitively rule out this possibility, however we support the visual vector inversion hypothesis rather than the “early motor vector” inversion hypothesis, because the latter presents several limitations. First, if the inverted motor vector were not adapted, then the motor vector inverted during antisaccade preparation would not be the final vector actually driving the saccade. If the representation that is inverted does not correspond to the metrics of the saccade but is more closely related to the position of the relevant saccade target, then it seems that such an “early motor” representation is actually a visual representation. Second, in addition to extensive neurophysiological evidence showing that adaptation is present in the cerebellum (Barash et al. 1999; Robinson, Fuchs & Noto, 2002; Scudder & McGee, 2003; Inaba et al. 2003 ; Robinson & Noto, 2005; Catz et al. 2005; Soetdjo & Fuchs, 2006;) and in cerebellar inputs (Straube and Deubel, 1995; Collins...
et al. 2008), recent neurophysiological evidence has shown that adaptation is present in the superior colliculus (Takeichi et al. 2007). This could suggest that adaptation might even be present upstream of the superior colliculus, in brain areas that would code “early motor” representations such as the frontal eye fields (Noto et al. 1999; Hopp and Fuchs, 2006).

Independently of this debate, our results inform about the relative timing of the vector inversion and adaptation processes. Our results suggest that the process of inverting a response to a visual target into activity in the contralateral hemisphere to the opposite location (i.e. the programming of the antisaccade) precedes the adaptive modification of the saccade vector in time. The idea that the vector inversion precedes adaptation is compatible with current thinking about the neural substrates of the two processes: vector inversion could take place in LIP (e.g. Barash & Zhang, 2006) or prefrontal cortex (Funahashi et al. 1993) and adaptation in the cerebellum.

In conclusion, our results show that the vector inversion made during antisaccade preparation precedes the adaptive modification of the motor vector. They also suggest that the inversion process could be that of transforming a visual representation in one hemifield into a visual representation in the other. Such visual vector inversion could be linked to parietal visual activity in response to a target in the hemifield opposite the receptive field when an antisaccade was to be made (Zhang and Barash, 2000; 2004).

ACKNOWLEDGMENTS:
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REFERENCES


Hopp J, Fuchs A. Amplitude adaptation occurs where a saccade is represented as a vector and not as its components. Vision Res 46: 3121-8, 2006.


FIGURE CAPTIONS

**Figure 1. Four saccade types and hypotheses.** Two left columns: Four saccade types. The adapted saccade was directed to a visual target placed 6° to the right (V+M+). The signs (+) and (-) are used to indicate whether the visual target and/or the motor vector of the required response were to the same (+) or opposite (-) side as the adapted saccade. Thus, the other saccades could be directed towards the right (M+) or to the left (M-) and be guided by a saccade target on the right (V+) or on the left (V-). Prosaccades (V+M+ and V-M-) are in shaded boxes. Two right columns: predictions of the two alternative hypotheses (visual versus motor vector inversion) about the transfer of rightward prosaccade adaptation to other saccades.

**Figure 2. Saccade gain and latency (Exp 1)** for the five successive phases: pre-tests (anti- and prosaccades), adaptation and post-tests (pro- and antisaccades). Data is presented separately for saccades directed to left and to the right. Error bars represent standard deviation across the seven subjects.

**Figure 3. Saccadic adaptation (Exp 1).** Individual time course (Subject 6, first replication): saccade gain as a function of trial number in pre-test, adaptation and post-test phases, for prosaccades (circles) and antisaccades (crosses). Each data point represents one saccade. The upper part of the graph shows saccades to the right and the lower part saccades to the left.

**Figure 4. Adaptation transfer (Exp 1)** for the four saccade types, over the seven subjects (larger panel, with error bars representing standard deviation) for each of the seven subjects (lower panels), as a function of the target position (to the left or right). Adaptation transfer to rightward prosaccades was set at 100% for all subjects.

**Figure 5. Saccade latency and gain (Exp 2)** for the five successive phases: pre-tests (pro- and antisaccades), adaptation and post-tests (anti- and prosaccades). Pro-saccades are shaded in gray and antisaccades in white. Data is presented separately for saccades directed to the six possible saccade targets (-8°, -6°, -4°, +4°, +6°, +8°). Error bars represent standard deviation across the seven subjects.

**Figure 6. Saccadic adaptation (Exp 2)** in an individual leftward adaptation session (Subject 5): saccade amplitude as a function of trial number, for pro- and antisaccades evoked by targets at -8°, -6°, -4°, 8°, 6° and 4°. Each data point represents one saccade. The three phases (pre-test, adaptation, post-test) are distinguished by dashed vertical lines. The upper part of the graph shows saccades to the right and the lower part saccades to the left.

**Figure 7. Adaptation transfer (Exp 2)** for leftward (A) and rightward (B) adaptation sessions as a function of saccade type (prosaccades; antisaccades) and target eccentricity (±4, 6, 8). Average
results + standard deviation (top panels) and individual results (bottom panels, each histogram represents one subject) are shown.
TABLE 1.

<table>
<thead>
<tr>
<th>Visual vector inversion</th>
<th>Motor vector inversion</th>
</tr>
</thead>
<tbody>
<tr>
<td>V+ M+  Pro</td>
<td>Adaptation</td>
</tr>
<tr>
<td>V+ M-  Anti</td>
<td>No transfer</td>
</tr>
<tr>
<td>V- M-  Pro</td>
<td>No transfer</td>
</tr>
<tr>
<td>V- M+  Anti</td>
<td>Transfer</td>
</tr>
</tbody>
</table>

**Figure 1.**
Figure 2
Figure 3

Pre-test Adaptation Post-test

Gain

Rightward saccades

Leftward saccades

X antisaccades
○ prosaccades
Figure 4
Figure 5
Figure 6
Figure 7

A) Leftward adaptation

B) Rightward adaptation