



Eye movement signals influence perception: Evidence from the adaptation of reactive and volitional saccades

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Abstract

Information about upcoming saccadic eye movements is used to orient visuo-spatial attention across the visual field. Different eye movement signals (intended or actual) could be used according to the intentionality of the saccade in preparation (Reactive or Volitional), and can be dissociated by saccadic adaptation. Gap 0 and overlap paradigms were contrasted to elicit the two saccade populations with different latencies and an asymmetric transfer of saccadic adaptation. Preparation of both saccade types caused a concomitant shift in the attentional focus (indexed by relative perceptual performance) to the actual, not intended, eye position. The attentional shift emerged progressively, earlier for V-saccades but reaching a maximal level around saccade onset for both saccade types. These results suggest that information about actual eye movements mediates the pre-saccadic shift of attention.

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1. Introduction

1.1. Visuo-spatial attention and saccade programming

Visuo-spatial attention is directed towards the location the eyes are aiming for. This spatial coupling has been shown using behavioral methods, where relative perceptual performance across the visual field is taken as an indicator of the focus of attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995). Neurophysiological approaches have also shown that activation of certain areas of the saccadic system orients attention (Moore & Fallah, 2001, 2004), or that prior orienting of attention influences the direction of the upcoming saccade (Kustov & Robinson, 1996). These studies suggest that information about eye movements is used by the perceptual system. However, the question of whether

the intended or the actual eye movement signal (EMS) is used to orient attention is still under debate. The intended EMS represents the movement necessary to attain the saccade target whereas the actual EMS represents the executed movement. These EMS are generally similar but can differ because of oculomotor error. Previous work using a paradigm in which there was an instructed saccade target found that best perceptual performance was coupled with the intended saccade target rather than the actual saccade endpoint (Deubel & Schneider, 1996). In a paradigm where subjects were allowed to aim freely within the spatially extended target, best perceptual performance was coupled with the actual saccade endpoint (Doré-Mazars, Pouget, & Beauvillain, 2004). Both studies confirm the preponderant role of saccade programming in attentional orienting, but neither was designed to dissociate the intended from the actual EMS. If attention were linked to the former, attention and saccade programming could be independent but functionally coupled processes. If attention were linked to the latter, the orientation of attention before the saccade would be the result of a specific motor computation.

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1.2. Saccadic adaptation

A way to assess the weight of motor programming in the relationship between attention and saccade preparation is to measure perceptual performance at both the intended saccade target position and the actual endpoint during the preparation of a saccade. Most of the time, these two positions are very similar, but they can be dissociated by saccadic adaptation, the progressive modification of amplitude to correct systematic targeting errors. Adaptation can be observed in patients recovering from dysmetria after extraocular muscle damage (e.g. Abel, Schmidt, Dell’Osso, & Daroff, 1978), but can also be induced in normal subjects by a double-step procedure during which the saccade target is systematically stepped forward or backward during the saccade (e.g. Deubel, Wolf, & Hauske, 1986; McLaughlin, 1967). Due to the inability of human subjects to detect small target displacements during saccades (Bridgeman, Hendry, & Stark, 1975), the target step is imperceptible. Nevertheless, after several trials saccadic amplitude adapts to the intra-saccadic shift, thus dissociating the actual endpoint from the intended position.

1.3. Perceptual consequences of saccadic adaptation

Previous experiments found perceptual consequences of saccadic adaptation with different perceptual tasks. For example, in the Bahcall and Kowler (1999) study, subjects had to estimate the localization of a post-saccadic probe in relation to the position of the pre-saccadic target. Before adaptation, localization was veridical, but after adaptation, subjects mislocalized the probe in the direction of the amplitude shift, that is, toward the actual endpoint. Bahcall and Kowler (1999) interpreted their results as showing that the efference copy of the EMS used for perception did not take adaptation into account. However, their results can also be explained by assuming that adaptation led to the reorganization of the representation of space (see also Hopp & Fuchs, 2004, for a similar point of view). In line with such an interpretation, Moidell and Bedell (1988) observed small but significant shifts in the localization of visual targets after adaptation. A similar result was found by Awater, Burr, Lappe, Concetta Morone, and Goldberg (2005) who examined localization of visual targets at the time of a saccade in order to assess whether peri-saccadic compression of space (systematic mislocalization of visual targets toward the saccade target) was focussed around the intended saccade target or the actual saccade endpoint. Their results showed that the focus of compression shifts with adaptation, to the actual endpoint. Mack, Fendrich, and Pleune (1978) showed that the threshold for detecting the direction of motion of a visual target was affected by adaptation. When horizontal saccades were adapted to acquire a vertical component, the detection threshold increased for motion in the direction of the amplitude shift and decreased for opposite motion.

A study using a discrimination task showed that the focus of attention did not shift with saccadic adaptation (Ditterich, Eggert, & Straube, 2000b) but was tied to the intended saccade target. This suggested that signals downstream from adaptation (representing actual movement) were not used to orient attention. Contradicting results were found by a study combining saccadic adaptation and a discrimination task and showing that when saccadic amplitude was adaptively modified, the focus of attention shifted in the direction of the amplitude shift (Doré-Mazars & Collins, 2005). The orientation of attention seems therefore to be tied to the endpoint of the saccade vector actually executed, and not to the intended presaccadic target, suggesting that the perceptual system must have access—as the saccadic system does (Sommer & Wurtz, 2002; Tanaka, 2003)—to precise information regarding the executed action. A possible explanation for the divergent results is related to the type of saccade elicited. Indeed, while Doré-Mazars and Collins’ (2005) experiment called for volitional saccades (V-saccades), the paradigm used by Ditterich et al. (2000b) called for reactive saccades (R-saccades).

1.4. Differences between V- and R-saccades

V- and R-saccades differ on several points. First, they are not elicited by the same stimulations. R-saccades are provoked by the sudden appearance of a peripheral target, which “automatically” evokes the saccade. These types of saccades have therefore traditionally been studied using the gap 0 paradigm (Mayfrank, Mobashery, Kimmig, & Fischer, 1986), where the disappearance of the foveal target and the appearance of the peripheral target are simultaneous. V-saccades are intentionally directed towards a permanent visual target which does not produce any transient signal susceptible of attracting a saccade. V-saccades have been studied using paradigms where foveal and peripheral targets are present simultaneously. The go-signal for the saccade is given by the offset of the fixation point after a certain time or by another stimulus such as a tone (overlap), or the saccade is self-paced (scanning). Second, the latency of R- and V-saccades differs. Typically, latency distributions for R-saccades peak around 180 ms, whereas they peak around 250 ms for V-saccades (Becker, 1989; Fischer, 1986). These differences in latency probably result from different neural programming pathways (Pierrot-Deseilligny, Rivaud, Gaymard, Muri, & Vermersch, 1995). The demonstration of different pathways for different saccades according to their intentionality comes essentially from studies showing that frontal eye field (FEF) lesions lead to deficits in triggering V-saccades and in inhibiting unwanted R-saccades, but not in triggering R-saccades; and that parietal eye field (PEF) lesions lead to R-saccade deficits but not to V-saccade deficits (Curtis & D’Esposito, 2003; Guitton, Buchtel, & Douglas, 1985; Heide & Kömpf, 1998; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Lynch & McLaren, 1989; Rivaud, Muri, Gaymard, Vermersch, & Pierrot-Deseilligny, 1994). Imaging techniques have also

shown more FEF activation during the preparation of V-saccades relative to R-saccades which are associated with specific inferior parietal activation (Mort et al., 2003). Furthermore, even if both saccades can be adapted, the adaptation of one type of saccade does not fully transfer to the other (Deubel, 1995; Erkelens & Hulleman, 1993; Fujita, Amagai, Minakawa, & Aoki, 2002), suggesting that adaptation of V- and R-saccades takes place at different sites (Deubel, 1999; Gancarz & Grossberg, 1999).

The role of motor programming in the orientation of attention could depend on the amount of time the saccadic system needs to program the saccade. V-saccades' longer latency may allow enough time for motor modifications arising late in the oculomotor pathways (such as adaptation) to be taken into account in selecting the target for perception. R-saccades' shorter latency may not leave enough time, consequently the intended target position would be selected by the perceptual system. In other words, if the perceptual effect of adaptation shown by Doré-Mazars and Collins (2005) results from the perceptual system's use of actual eye movement signals, it is possible that these signals are not always relayed to higher brain areas involved in perception.

1.5. Goal of the present study

The goal of the present study was to assess the role of saccade intentionality (volitional vs. reactive) in the effect of saccadic adaptation on perception. In separate sessions, gap 0 and overlap 300 paradigms were used to elicit R- and V-saccades, respectively. For each session, there were two successive phases: pre-adaptation and adaptation. In the latter, the peripheral stimulus was shifted backward by 1° of visual angle during the saccade toward it, in order to evoke saccadic adaptation. In the first experiment, participants had to saccade toward a peripheral stimulus, and then perform a discrimination task about the orientation of a single oblique line embedded with distracters and presented briefly within this peripheral contour just before R- or V-saccade onset. In the second experiment, we verified that the perceptual effect was the result of the intentionality of the saccade, and not due to timing differences in the paradigms used to elicit R- vs. V-saccades. In the third experiment, we verified that these paradigms did indeed elicit two different populations of saccades by examining the transfer of V-saccade adaptation to R-saccades, and vice versa.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Four naive participants and one of the authors were tested. All had normal or corrected-to-normal vision and were familiar with the eye-movement recording apparatus and calibration procedure.

2.1.2. Eye movement recording

The stimuli were presented on a Hewlett-Packard 1310A CRT (P15 phosphor) display interfaced with a fast graphic system providing a frame frequency of 1000 Hz. Eye movements were monitored by a Bouis Oculomotor system (Bach, Bouis, & Fischer, 1983), with an absolute resolution of 6 arcmin and a linear output over 12° of visual angle. Each session began with the calibration of the eye-tracking system in which participants sequentially fixated five positions along a horizontal 12° -long axis. In addition, calibration accuracy was checked at the beginning and the end of each experimental trial by means of a fixation bar 6° to the left and to the right of the screen center. Saccades made during this calibration check were about 8° , sufficiently different from the saccades examined during the experimental trials to minimize the interference of the calibration check on the adaptive process. Viewing was binocular but only the movements of the right eye were monitored, and signal from the eye tracker was sampled every two ms. The beginning and end of a saccade were detected by the time derivative of the voltage signal sampled by the eye tracker and the graphics interface that control the scope allowed a change of display in one ms. Consequently, the intra-saccadic step occurred less than 8 ms after the saccade was detected, before the saccade reached its endpoint (saccade duration 20–30 ms). Participants were seated 70 cm away from the screen and their head kept stable with a submaxillary dental print and forehead rest. Further details of the eye movement recording apparatus, calibration procedure and numerical data processing can be found in Beauvillain and Beauvillain (1995).

2.1.3. Visual stimuli

The visual stimuli consisted of two open-ended contours (Fig. 1A), a short foveal fixation contour ($1^\circ \times 0.5^\circ$) and, 2° to the right, a longer peripheral contour ($1^\circ \times 4.5^\circ$). They were green on a black background, and their apparent luminance was set at 0.45 cd/m^2 at the beginning of each experimental block with a Minolta LS-110 luminance-meter.

In order to probe perceptual capabilities at different positions in the visual field during the preparation of a saccade, nine line segments—four horizontal and four vertical distracters (– and |) and the single oblique line (\ or /) — appeared briefly in the peripheral contour. The oblique line was the discrimination target (DT) and it appeared randomly, with equal probability, either at the second position (P2) or the fourth position (P4) of the line segment chain. Presenting distracters with the DT ensured that the abrupt DT onset did not “pop out” from the display and automatically attract the saccade or attention to its position (Irwin, Colcombe, Kramer, & Hahn, 2000; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Furthermore, the DT was always flanked by two different distracters (one horizontal and one vertical), and distracters alternated every position (see example in Fig. 1A).

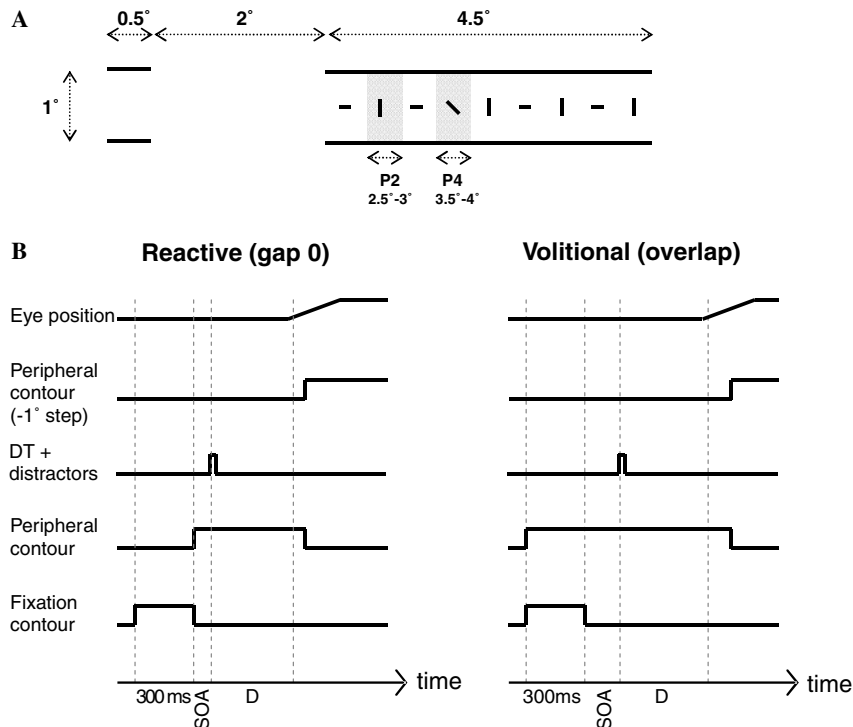


Fig. 1. Stimuli and procedure. (A) Visual stimuli included a small fixation contour and a longer peripheral contour which was empty except for the 30 ms presentation of the line segments (DT and distracters), as illustrated here. The shaded regions (not visible during stimulus presentation) correspond to positions P2 and P4. In Experiment 3, the line segments were not presented. (B) Experimental procedure. For eliciting R-saccades, subjects had to fixate the small foveal contour until the peripheral contour appeared 300 ms later, simultaneous with foveal contour offset. After a fixed SOA (100 ms) and before saccade onset, the line segments appeared for 30 ms inside the peripheral contour, and then the contour remained empty for the rest of the saccadic latency and throughout the rest of the trial. The procedure for eliciting V-saccades was similar, except that both contours appeared at the same time and subjects had to withhold their saccade until foveal contour offset 300 ms later. In Experiment 1, the SOA between the go-signal and line segment presentation was 140 ms. In Experiment 2, the SOA was 140 or 100 ms with equal probability. For all adaptation trials, the peripheral contour was stepped 1° to the left during the saccade directed toward it. For pre-adaptation trials, there was no such step. On the time line the SOA (time between go-signal and DT presentation) and D (delay between DT presentation and saccade onset) are indicated.

The endpoints of saccades directed toward a spatially extended target or to several grouped targets are variable but tend to land on a central position within the visual configuration, called the “center of gravity” (Coren & Hoenig, 1972). When the visual properties of the targets differ, the global characteristics of the configuration determine the endpoint. If one element is larger or more intense then the saccade lands closer to that target in comparison to condition in which the two elements are identical (Deubel, Wolf, & Hauske, 1984; Findlay, 1982). Furthermore, more weight is given to those elements of the configuration which are closer to the center of the field. This center of gravity effect may be the result of a spatio-temporal averaging of the retinal luminance configuration (Deubel et al., 1984), and of a cortical magnification factor (Rovamo, Virsu, & Nasanen, 1978). In the present experiments, the geometric center of the peripheral contour was position 5 (centered on 4.25° from the fovea) but saccade endpoints were expected to fall on P4 for the aforementioned reasons. Indeed, preliminary observations confirmed that P4 corresponded to the average pre-adapted saccade endpoint and P2 to the average adapted saccade endpoint. The two DT locations, P2 and P4 (centered on 2.75° and 3.75°), were then selected accordingly.

The eccentricity of the peripheral contour (2°) and the average saccade amplitude necessary to attaining its center (4.5°) were chosen for the following reasons. First, as the perceptual test was performed before saccade onset, when the fovea was still on the fixation contour to the left, such a small distance ensured that acuity limitations did not produce a floor effect. Furthermore, 4.5° remains within the range of eccentricities usually used in experiments testing perceptual capabilities as a function of saccade programming (e.g. Deubel & Schneider, 1996; Kowler et al., 1995). Finally, the brief presentation time (30 ms) of the distracter + DT chain avoided discrimination performance ceiling effects at this eccentricity while allowing the test to be compatible with saccadic latency.

Because of the relatively high number of observations necessary for calculating meaningful percent correct discrimination performance per DT position and saccade type, a constant eccentricity and intra-saccadic target step (-1°) were chosen to evoke optimal amounts of adaptation within the fewest trials. Such a constant eccentricity and intra-saccadic step have been shown to speed the rate of adaptation (Miller, Anstis, & Templeton, 1981; Scudder, Batourina, & Tunder, 1998). Such a procedure allowed us

to rapidly differentiate pre-adaptation from adaptation phases, as this was what operationalized the coincidence between saccade endpoints and different DT positions.

2.1.4. Procedure

The procedure for eliciting R-saccades was as follows (Fig. 1B left): after calibration of the eye-movement recording apparatus, the foveal contour appeared. Participants had to fixate it and make a saccade toward the peripheral contour as soon as it appeared (300 ms later, simultaneous to foveal contour extinction), always to the right. One hundred milliseconds later (stimulus onset asynchrony, SOA 100), the line segments appeared for 30 ms, and then the contour remained empty for the rest of the saccadic latency until the subject's response. The procedure for eliciting V-saccades was identical, except that both the foveal and the peripheral contours appeared simultaneously (Fig. 1B right). Subjects had to withhold their saccade toward the peripheral contour until the go-signal for the saccade (foveal offset), by which time foveal and peripheral targets had overlapped for 300 ms. After an SOA of 140 ms, the line segments appeared for 30 ms. For both procedures, participants indicated the orientation of the oblique (left or right) after their saccade by pressing on the corresponding one of two buttons placed in front of them. They were under no time pressure to give their response, as we wanted to avoid the slowing of the saccadic motor response as a result of bottleneck processing of two simultaneous actions even if oculomotor actions seem to be relatively free of such interference (Pashler, Carrier, & Hoffman, 1993). Finally, each trial ended with a calibration check.

The exact timing of DT presentation must be taken into account when examining discrimination performance. Two indicators could be used here: either the time of DT presentation from the beginning of saccade latency or the delay (D) between DT presentation and saccade onset. The first is controlled by SOA. The second can only be inferred after the saccade because it depends on latency which varies stochastically. The timing of DT presentation relative to saccade onset has been shown to affect perceptual performance (Doré-Mazars et al., 2004), with the coupling between saccade endpoint and position of best perceptual performance appearing around 150 ms before saccade onset and becoming decisive in the last 100 ms of oculomotor programming. In the present experiment, in order to test discrimination performance around this time for both saccade types, DT was presented 140 ms after the go-signal for V-saccades, and 100 ms for R-saccades. Delay between DT display and saccade onset was 126 ± 15 and 119 ± 17 ms (average \pm SD) for V- and R-saccades respectively. The small 7 ms difference reached significance ($F(1,4) = 15.3$, $p < .02$), but for both saccade types delay was in the range within which perceptual effects were expected.

2.1.5. Design

Each experimental session began with 96 pre-adaptation trials with no intra-saccadic shift and determined sac-

cade characteristics in the dual task used here. The 120 following trials were adaptation trials with the intra-saccadic displacement of the peripheral contour. One experimental session therefore consisted in 216 trials. Trials were organized pseudo-randomly in such a fashion that each DT position (P2 or P4) was tested 4 times every 8 trials. Six sessions were run for each subject, three for each saccade type, and the order of saccade type was counterbalanced across subjects. Sessions were separated by 3–5 days and we did not observe any persistence of adaptation between sessions.

2.2. Results

Overall, 29% of the trials were excluded from the analyses for the following reasons: lack of accuracy in the eye position measurement, blinks, or trials in which a saccade was triggered during the SOA, DT presentation, or up to 30 ms after DT extinction. Furthermore, 10% of the pre-adaptation trials were discarded because the saccade landed closer to P2 than to P4. Finally, in order to avoid including in the analyses of variance trials in which adaptation was only beginning, we omitted the first 24 trials of the adaptation phase. During the rest of the adaptation phase, there were a few observations closer to P4 than to P2, but not consistently for all subjects. For each dependant variable, a 2 (phase, pre-adaptation vs. adaptation) \times 2 (DT position, P2 vs. P4) \times 2 (saccade type, volitional vs. reactive) univariate ANOVA was carried out. *p*-values are given in parentheses and when indicated, *T*-tests were also performed.

2.2.1. Saccade latencies

The overlap paradigm elicited saccades with average (\pm SD) latencies of 267 ± 16 ms, and the gap 0 paradigm elicited saccades with average latencies of 223 ± 13 ms. The difference was significant ($F(1,4) = 553.1$, $p < .0002$), suggesting that the paradigms elicited two distinct populations of saccades (V- and R-saccades respectively) as illustrated in Fig. 2 (top) presenting V- and R-saccade latencies as a function of trial number for one representative subject. Phase and DT position did not affect latency ($F_s < 1$). Latency was longer than that usually observed with saccades in a single saccade task (i.e. without a concurrent perceptual task, see also Experiment 3). At least two explanations can account for this. First, elimination criteria based on latency (saccades whose onset occurred during the SOA, DT presentation or up to 30 ms thereafter) resulted in the elimination of the shortest latencies (< 160 and < 200 ms for R- and V-saccades, respectively). Nevertheless, the great majority of the data was above this criterion. Second, saccade latency is longer when the task load is greater, such as when the saccade is coupled with a perceptual task (Deubel & Schneider, 1996; Stuyven, Van der Goten, Vandierendonck, Claeys, & Crevits, 2000). In spite of this, the latency difference between R- and V-saccades remained in the normal range.

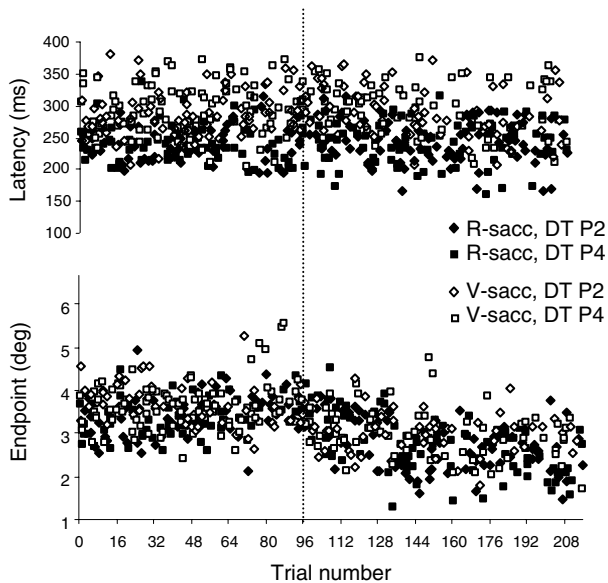


Fig. 2. Experiment 1. Saccade latencies (milliseconds) and endpoints (degrees) as a function of trial number for V- and R-saccades and for the two DT positions (P2 and P4), in one subject. Note that DT positions P2 and P4 spanned 0.5° and were centered on 2.75° and 3.75° , respectively, and that the adaptation phase started from trial 97 (indicated by the dotted vertical line).

2.2.2. Saccade endpoints

ANOVA revealed that R- and V-saccade endpoints did not differ significantly from each other ($F(1,4) = 3.3$, $p > .14$) but both were modified by the intra-saccadic target step ($F(1,4) = 301.5$, $p < .0003$). No interaction was found between the two factors ($F(1,4) = 1.5$, $p > .29$). DT position did not affect endpoints ($F < 1$), and there was no interaction between DT position and phase ($F < 1$), confirming that subjects did not aim for DTs but for the contour as a whole. This was expected because of the moment and duration of DT presentation during saccade latency, and because DT did not pop out from distracters. Average endpoints were $3.8^\circ \pm 0.1^\circ$ and $3.8^\circ \pm 0.2^\circ$ in the pre-adaptation phase,¹ and $2.8^\circ \pm 0.3^\circ$ and $2.6^\circ \pm 0.2^\circ$ in the adaptation phase, for V- and R-saccades, respectively. Fig. 2 (bottom) presents the time course of adaptation for one subject. Each data point represents an individual trial obtained in a single session. Endpoints shifted progressively but rapidly leftward after the introduction of the intra-saccadic target step.

The rate of adaptation in each individual experimental session was modeled with an exponential (average $R^2 = 0.22$), allowing an estimate of the number of trials necessary for attaining the adapted endpoint (rate constants). The average rate constant for V-saccades was 20 trials, and 26 trials for R-saccades. Thus, the saccadic

adaptation rate was fast but progressive, probably due to the procedure and to the type of saccade target, a spatially extended stimulus. Indeed, the rate of adaptation could be faster with such stimuli than for single point targets (Ditterich, Eggert, & Straube, 2000a; Doré-Mazars & Collins, 2005), probably because of the greater retinal error generated by these stimuli. However, there were only very few corrective saccades. For the first 40 trials of the adaptation phase, $4 \pm 6\%$ of R-saccades and $5 \pm 3\%$ of V-saccades were followed by a corrective second saccade. Such a small proportion of corrective saccades with spatially extended targets has been reported before (Bahcall & Kowler, 1999) suggesting that corrective saccades do not play an important role in saccadic adaptation (Noto & Robinson, 2001).

Saccade endpoints were similar for V- and R- saccades. Before adaptation, 90% of observations corresponded to the center of gravity of the spatially extended stimuli. The systematic intrasaccadic backward step caused a rapid and progressive leftward shift in a similar way for both saccade types. At the end of the adaptation phase, the saccade compensated for the intrasaccadic step. We assumed that the intended EMS (the center of gravity of the parafoveal contour) and the actual EMS coincided in the pre-adaptation phase while they differed during the adaptation phase. We can now examine the role of saccade programming in the orientation of the presaccadic focus of attention by measuring perceptual capabilities just before saccade execution at positions corresponding to the future endpoint of the non-adapted or the adapted saccade.

2.2.3. Discrimination performance

While discrimination performance did not differ between R- and V-saccades ($F < 1$), it depended on both DT position and phase, as revealed by a significant interaction between these two factors ($F(1,4) = 58.7$, $p < .005$). This interaction reflects the fact that DTs appearing in P4 were better discriminated than DTs appearing in P2 ($F(1,4) = 27.4$, $p < .008$) during the pre-adaptation condition, and that the opposite pattern was observed during the adaptation condition: DTs appearing in P2 were better discriminated than DTs appearing in P4 ($F(1,4) = 35.4$, $p < .005$). As previously reported for non-adapted saccades, saccade programming prevails over acuity limitations as perceptual performance at the more peripheral position is better than at the close DT position when the saccade lands on the far position. The phase \times DT position interaction was significant for both V- and R-saccades ($F(1,4) = 110.0$, $p < .005$ and $F(1,4) = 15.3$, $p < .01$ respectively) but the triple DT position \times phase \times saccade type interaction failed to reach significance ($F(1,4) = 4.6$, $p > .09$). Whereas the difference between pre- and adaptation conditions was significant for both DT positions for V-saccades (-14% and $+13\%$ for P2 and P4, $F(1,4) = 38.5$ and $F(1,4) = 58.6$, $ps < .005$), this was not the case for R-saccades (-9% and $+8\%$ for P2 and P4, $F(1,4) = 2.2$, $p > .20$; $F < 1$), probably the result of the greater variability of performance in this condition (cf. Table 1). In order to further investigate

¹ Recall that the average saccade endpoint in the pre-adaptation phase does not take into account endpoints closer to P2 than to P4, leading to a small overestimation of the amount of adaptation.

Table 1

Average saccade latency (time from go-signal to onset, in milliseconds), saccade endpoint (distance from fixation point, in degrees) and discrimination performance (percent correct) according to saccade type (volitional or reactive), phase (pre-adaptation or adaptation) and DT position (P2 or P4)

	V-saccades				R-saccades			
	Pre-adaptation		Adaptation		Pre-adaptation		Adaptation	
	P2	P4	P2	P4	P2	P4	P2	P4
Latency	263 (18)	265 (21)	269 (15)	269 (15)	226 (11)	226 (11)	221 (15)	221 (15)
Saccade endpoint	3.8 (0.1)	3.8 (0.1)	2.8 (0.3)	2.8 (0.3)	3.8 (0.1)	3.8 (0.2)	2.6 (0.2)	2.6 (0.1)
Discrimination	69 (4)	84 (2)	83 (5)	71 (4)	68 (12)	78 (13)	77 (11)	70 (12)

DT positions P2 and P4 spanned 2.5°–3.0° and 3.5°–4.0°, respectively. Standard deviations are in parentheses. Each average is based on about 100 trials per subject.

differences between R- and V-saccades, we examined discrimination performance as a function of the delay between DT presentation and saccade onset. Even if SOAs were chosen to measure performance at short delays for which the saccade and attention coupling is strongest, latencies remained sufficiently variable to allow finer performance analyses as a function of delay to be carried out. To do so, data was partitioned into four 40-ms delay bins (41–80 ms, 13% of data both for R- and V-saccades; 81–120 ms, 47 and 32%; 121–160 ms, 29% and 36%; 161–200 ms, 9% and 15%; the smallest bin contained 20 data points).

For each delay bin, correct discrimination of targets appearing in each DT position (P2 or P4) was calculated for each phase (pre- or adaptation). The benefit of landing on the DT position was then calculated by comparing performance for the phase during which the saccade landed on the DT position (i.e. pre-adaptation for P4 and adaptation for P2) to the phase during which the saccade did not land on the DT position (i.e. adaptation for P4 and pre-adaptation for P2). The resulting difference corresponded to the spatial coincidence effect. While values close to 0 indicate that there was no difference in performance whether the endpoint of the upcoming saccade coincided or not with the DT position, positive values indicate a benefit of spatial coincidence between saccade endpoint and DT in that perceptual performance for a DT at a given position was enhanced when the saccade landed on it.

Fig. 3 presents the spatial coincidence effect for both saccade types. A 2 (DT position, P2 vs. P4) \times 2 (saccade type, reactive vs. volitional) \times 4 (delay: 41–80; 81–120; 121–160; and 161–200 ms) univariate ANOVA was performed. There was a global effect of delay ($F(3,12)=4.4, p<.03$), indicating a progressive benefit of the spatial coincidence between saccade endpoint and DT position as the delay became shorter and DTs were presented close to the time of saccade onset. There was neither an effect of DT position nor an interaction between delay and DT position ($F_s < 1$), indicating that the benefit of a saccade endpoint on the DT position was similar for the closer and farther DT positions. Globally, the effect of saccade type was marginally significant ($F(1,4)=5.7, p<.08$). In order to investigate this difference more thoroughly, each delay class will be presented successively.

At the shortest delays (41–80 ms before saccade onset), perceptual performance was enhanced when the saccade

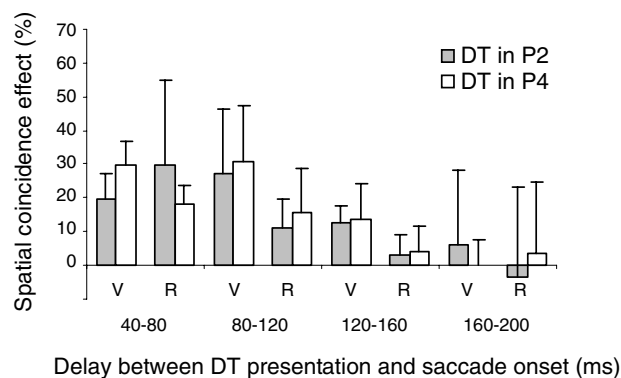


Fig. 3. Experiment 1. Effect of spatial coincidence between saccade endpoint and DT position for V- and R-saccades as a function of the delay between DT presentation and saccade onset. Positive values indicate an enhancement of perceptual performance for a DT position (P2 or P4) produced by a spatial coincidence with the saccade endpoint compared to no coincidence. (Recall that saccade endpoints in the pre-adaptation and adaptation phases coincide with DT positions P4 and P2 respectively). Each condition was based on at least 10 observations per subject. Error bars indicate +1 between-subject (SD).

endpoint coincided with the DT position compared with when the saccade endpoint did not coincide with the DT position. Indeed, there was a significant positive spatial coincidence effect for all DTs and both saccade types (T -tests, $p < .05$), with no difference between V- and R-saccades ($F < 1$).

At the longest delays (161–200 ms before saccade onset), no effect of coincidence was observed (values not different from 0, T -tests, $p > .10$), indicating that when the DT appeared during the early stages of saccade preparation, there was no effect of the upcoming saccade endpoint calculation on perceptual performance. There was no difference between R- and V-saccades,² nor between DT positions ($F_s < 1$).

² At the longest delays, correct discrimination performance was around 70% for both saccade types and was affected neither by DT position nor by phase. These two factors interacted at the shortest delays, as performance was around 80% and 65% for DTs occupying or not the same position as the endpoint of the upcoming saccade. Such an interaction indicates a selective spatial coupling just before the saccade onset and suggests that saccade programming produces a perceptual enhancement at the saccade endpoint at the expense of other locations.

Differences between saccade types arose for the two intermediate delay classes ($F(1,4) = 8.3, p < .045$ for the 81–120 ms class and $F(1,4) = 10.7, p < .035$ for the 121–160 ms class). For saccades occurring 81–120 ms after DT presentation, there was an effect of the upcoming endpoint on perceptual performance. Indeed, for both saccade types, there was a significant positive coincidence effect (T -tests, $p < .05$). The significant difference between the saccade types arose from the fact that the benefit was greater for V- (globally +29%) than for R-saccades (globally +13%). Finally, for saccades occurring 121–160 ms after DT presentation, there was an effect of the endpoint on perceptual performance when the upcoming saccade was volitional, but not when it was reactive, as the observed values in the latter case were not significantly different from 0 (T -tests, $p > .10$).

2.3. Discussion

For both V- and R-saccades, the pre-adaptation condition used in the present experiment replicates numerous studies showing a spatial coupling between saccade programming and perceptual performance (Kowler et al., 1995; Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996), and that the final stages of motor computation affect perception (Doré-Mazars et al., 2004). The present results show that the presaccadic shift of attention—as indexed by relative discrimination performance—is influenced by adaptive modifications of saccade amplitude. Again, this holds for both V- and R-saccades.

An alternative explanation for our results might be that instead of saccadic adaptation leading to a concomitant shift in attention, the intra-saccadic step might have an effect on attention which subsequently modifies saccade endpoints. Shifts of exogenous attention can indeed be adapted (McFadden, Khan, & Wallman, 2002) and following such adaptation saccade amplitude was smaller even though no saccades had been made during the adaptation phase. Note however that the subsequent saccadic adaptation was relatively small (only 6% gain change) and more importantly, the timing of the target shift to obtain an attentional adaptation was very different from that used in the present study. The precise timing is crucial to the adaptation of attention as a late target step (as was the case in the present experiment) cannot adapt attention. Another attentional effect that might influence saccade amplitude is that despite saccadic suppression subjects might become aware of the difference between pre-saccadic and post-saccadic contour locations and modify their saccade amplitude in anticipation of this. Several points argue against this interpretation. If adaptation were the result of a conscious targeting strategy, we would have expected to observe modifications of saccade latency for the initial adaptation trials, which was not the case. Indeed, saccades directed to positions other than the saccade target tend to have longer latencies, the most extreme example being antisaccades. In our situation, the saccade target was assumed to be the center of gravity, indeed it has also been shown that saccades

directed away from this position have longer latencies (Coëffé & O'Regan, 1987). Finally, none of the subjects reported being aware of the step, except one author on some trials, whose adaptation was progressive just like the other, naive subjects. Finally, recall that subjects were required to perform a dual task, saccade and discrimination. The perceptual task was relatively difficult as it concerned the orientation of an oblique line embedded among eight distracters, all briefly presented before saccade execution. The position of the DT was not predictable and a strategy consisting of selecting a particular saccade target (depending on trials without or with an intra-saccadic step) would not have been helpful in improving discrimination performance. For these reasons, we think that it was the saccadic adaptation that led to the concomitant shift in the locus of presaccadic attention, and not a potential attentional effect that led to the reduction in saccade amplitude.

The second result that emerges from this experiment is the time course of the spatial coupling between saccade preparation and attentional orienting. The spatial coupling emerges progressively, suggesting that the orientation of attention toward the next saccade endpoint occurs as saccade programming leads to the selection of this endpoint (Doré-Mazars et al., 2004). Best perceptual performance at the saccade endpoint emerged relatively early during the preparation of a V-saccade (around 140 ms before onset) but only later for R-saccades (around 100 ms before onset). It seems that the actual EMS that the perceptual system uses to orient attention before the saccade would be delivered earlier or faster to the perceptual system when a V-saccade is under preparation compared with a R-saccade.

Two points remain to be addressed before we can conclude that the differences observed in the present experiment result from the intentionality of the saccades (R- vs. V-saccades). These are addressed in Experiments 2 and 3.

3. Experiment 2

Because the only difference between R- and V-saccades concerns the time course of the spatial coupling between saccade and perceptual performance, it is important to verify that these differences resulted from the intentionality of the saccades, rather than from the time of DT presentation (SOA, time between the go-signal for the saccade and DT presentation). Indeed, as mentioned in the Section 2.1, in order to present DT at similar times before saccade onset, DT was presented 140 ms after the go-signal for V-saccades, and 100 ms after for R-saccades. Therefore, for V-saccades, the contour in which the DT subsequently appeared could be integrated longer than for R-saccades. Some authors have shown that the longer a stimulus is present, the more precise the saccades directed toward it become (Coëffé & O'Regan, 1987). Even if we did not find different R- vs. V-saccade endpoints, perhaps the greater integration time for V-saccades could also lead to an earlier effect on perception. While it must be noted that the DT was presented for 30 ms for both saccade types, we wanted

to make sure that the different time course between R- and V-saccades was not due to the difference in SOA. To do this, in Experiment 2, we asked the five participants to perform the same dual task (saccade and discrimination) in an overlap 300 paradigm during which DT could appear either 100 or 140 ms after the go-signal for the saccade in order to test performance at similar delays but with different integration times (SOA were randomly interleaved during a session). If the differences found between V- and R-saccades in Experiment 1 were related to the use of a different SOA, an effect of SOA on perceptual performance would be expected in the present experiment where only V-saccades are considered.

3.1. Methods

3.1.1. Participants, instruments and visual stimuli

The same five subjects as in Experiment 1 took part in Experiment 2. The instruments and visual stimuli were identical to those in Experiment 1 (see Fig. 1A).

3.1.2. Procedure

The procedure for eliciting V-saccades was identical to that used in Experiment 1 (see Fig. 1B), except that two SOA durations were tested in an interleaved manner: 100 ms and 140 ms.

3.1.3. Design

Each experimental session was composed of 248 trials, 112 pre-adaptation followed by 136 adaptation trials. Trials were organized pseudo-randomly in such a fashion that each target position (P2 or P4) was tested 4 times every 8 trials. Four sessions, separated by 3–5 days, were run per subject.

3.2. Results

Twenty-seven percent of trials were excluded for the same reasons as Experiment 1. Furthermore, in order to restrain analyses of variance to trials which clearly distinguished the phases in terms of endpoints, the averages did not include the first 24 trials of the adaptation phase, nor those pre-adaptation trials for which the endpoint was closer to P2 (13%). For each dependant variable, a 2 (phase, pre-adaptation vs. adaptation) \times 2 (DT position, P2 vs. P4) \times 2 (SOA, 100 vs. 140 ms) univariate ANOVA was carried out. p -values are given in parentheses and when indicated, T -tests were also performed.

3.2.1. Saccade characteristics

Saccade characteristics (latency and endpoints) were similar to those found for V-saccades in the previous experiment. Fig. 4 presents the time course of saccade latencies and endpoints for one representative subject.

Average pre-adaptation saccade endpoint was $3.8^\circ \pm 0.2^\circ$, and average adapted saccade endpoint was $2.7^\circ \pm 0.2^\circ$, the effect of phase was significant ($F(1,4) = 89.9, p < .001$). Neither

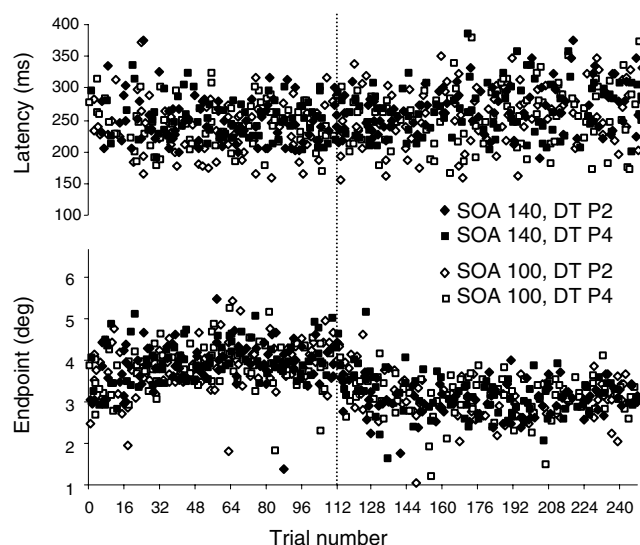


Fig. 4. Experiment 2. Saccade latencies (milliseconds) and endpoints (degrees) as a function of trial number for the two DT positions (P2 and P4) and the two SOAs (100 and 140 ms), for one subject. Each point corresponds to a single saccade. The adaptation phase started from trial 113 (indicated by the dotted vertical line).

the SOA nor DT position affected saccade endpoint ($F_s < 1$). As in Experiment 1, there were very few corrective saccades. For the first 40 trials of the adaptation phase, $1 \pm 2\%$ of saccades were followed by a corrective second saccade.

Average saccade latency was 270 ± 37 ms and there was no effect of phase ($F < 1$), SOA ($F(1,4) = 3.7, p > .12$) or DT position ($F < 1$), and no interaction reached significance (all $ps > .14$). As expected, delay (between DT presentation and saccade onset) depended on SOA ($F(1,4) = 16.2, p < .02$). Indeed, the average delay was $161 \text{ ms} \pm 32$ and 139 ± 40 ms in the 100 and 140 ms SOA conditions.

3.2.2. Discrimination performance

Discrimination performance did not depend on SOA ($F(1,4) = 1.9, p > .22$) but depended on both DT position and phase, as revealed by a significant interaction between these two factors ($F(1,4) = 30.1, p < .01$). SOA interacted neither with DT position ($F < 1$) nor with phase ($F(1,4) = 2.0, p > .22$) and the triple interaction did not reach significance ($F < 1$).

As in Experiment 1, data were partitioned into four 40-ms delay bins (41–80 ms, 7% and 19% of data for SOA 100 and 140 ms; 81–120 ms, 30% and 36%; 121–160 ms, 35% and 24%; 161–200 ms, 28% and 22%; the smallest bin contained 70 data points) and the spatial coincidence effect was calculated for each DT position as previously. The time course of the spatial coupling was not different between the two SOAs ($F < 1$), however there was a global effect of delay ($F(1,4) = 34.5, p < .001$) reflecting a greater spatial benefit effect as the delay became shorter (Fig. 5). As for the V-saccades in the first experiment, there was a spatial coincidence benefit for the first three delay classes (positive values different from 0, T -tests, $ps < .05$) that disappeared for the longest delay class, whatever the SOA.

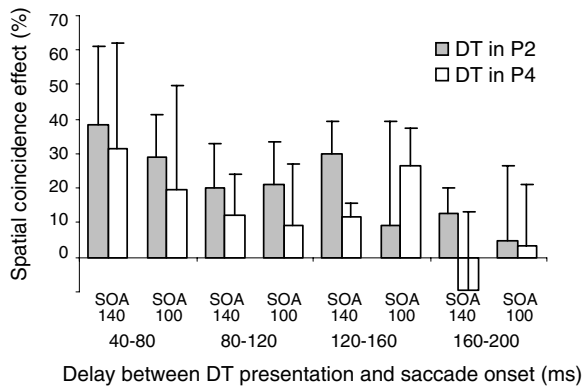


Fig. 5. Experiment 2. Effect of spatial coincidence between saccade endpoint and DT position for V-saccades with 100 or 140 ms SOA, as a function of the delay between DT presentation and saccade onset. (Recall that saccade endpoints in the pre-adaptation and adaptation phases coincide with DT positions P4 and P2, respectively). Each condition was based on at least 10 observations per subject. Error bars indicate +1 between-subject SD.

3.3. Discussion

Experiment 2 showed that the emergence of a spatial coupling between position of best perceptual performance and saccade endpoint does not depend on the moment of DT presentation relative to the go-signal for the V-saccade (SOA) but on the moment of DT presentation relative to saccade onset (D). The differences observed in Experiment 1 between R- and V-saccades cannot therefore be attributed to the different SOAs used in the gap 0 and overlap 300 paradigms, but appear to be tied to the intentionality of the saccade per se: the spatial coupling appears around 140 ms before the onset of the V-saccades and 100 ms before the onset of R-saccades.

In order to be fully confident that perception used an actual EMS during the preparation of both R- and V-saccades, it is crucial to demonstrate that our paradigms elicited different saccade types in addition to the observed latency difference. This was addressed in Experiment 3 by adapting one saccade type and testing whether the adaptation transferred to the other saccade type.

4. Experiment 3

A more robust test that our paradigms did indeed elicit R- vs. V-saccades would be a test of transfer of adaptation from one type to the other. Absence of transfer, or partial transfer, suggests that adaptation is specific to the adapted saccade type, and suggests programming differences between the adapted and tested saccades. While adaptation of one type of saccade transfers to saccades of the same category (normal reactive to express saccades, and vice versa, in gap 0 and gap 200–300 paradigms, Hopp & Fuchs, 2002; V-saccades in scanning to overlap, Deubel, 1995), the transfer of V-saccade adaptation to R-saccades and vice versa is unclear in the literature. Partial transfer of V-saccade adaptation to R-saccades has been observed

(Deubel, 1995; Erkelens & Hulleman, 1993; Fujita et al., 2002) but was absent for some subjects (Erkelens & Hulleman, 1993). Both no and partial transfer of R-saccade adaptation to V-saccades has been reported (Deubel, 1995; Fujita et al., 2002). Absence of transfer or partial transfer between saccade types remains an argument in favor of different neural mechanisms underlying the different types of saccades and, importantly for the present study, that different pathways were used to program the different saccades.

In addition to the transfer paradigm, the specificity of adaptation can be assessed by inducing different adapted states simultaneously for saccades with different characteristics. Although this was not the approach adopted here, this paradigm has been used to show, for example, that saccades of different directions can be differentially adapted (e.g. gain increase for leftward saccades vs. gain decrease for rightward saccades, Semmlow, Gauthier, & Vercher, 1989; Shelhamer & Clendaniel, 2002). The same is true for saccades of different amplitudes (gain increase for 5° saccades vs. gain decrease for 20° saccades, Miller et al., 1981). Finally, the saccadic system can, when pressured, develop different adaptation for different depths (gain increase for “far” 5° saccades vs. gain decrease for “near” 5° saccades, Chaturvedi & van Gisbergen, 1997) or for different eye positions (Alahyane & Pélisson, 2004) even though under normal circumstances adaptation is not specific to an eye position (Albano, 1996).

We adapted one type of saccade (either R- or V-) using the same paradigms as in the previous experiments (gap 0 and overlap 300), and tested whether the adaptation transferred to the other saccade type (V- or R-). The stimuli used were identical to those used previously (see Fig. 1A), with the exception that the line segments were not presented. Subjects simply had to saccade toward the spatially extended stimulus. For each saccade type, endpoint was compared before and after the adaptation of the other saccade type. Based on previous studies, we expected to find either an absence of transfer or incomplete transfer of adaptation between the two saccade types.

4.1. Methods

4.1.1. Participants

Ten subjects with normal vision participated in the experiment. Four had participated in both Experiments 1 and 2.

4.1.2. Instruments and visual stimuli

The instruments were the same as in Experiments 1 and 2.

The visual stimuli were also identical (see Fig. 1A) except that the line segments (DT and distracters) were never presented. Subjects had only one task, to saccade toward the spatially extended visual object. For the reasons outlined in Experiment 1, we expected the saccade target to be the center of gravity of the elongated peripheral contour.

4.1.3. Procedure

The procedure for eliciting R- and V-saccades was similar to the previous experiments, gap 0 and overlap 300, respectively. Each experimental session (220 trials) was divided into four successive phases: 40 Type 1 pre-test trials/40 Type 2 pre-test trials/100 Type 2 adaptation trials/40 Type 1 post-test trials. Both gap 0 and overlap 300 paradigms were tested as Type 1 and Type 2, the order was counterbalanced across subjects, and the sessions were separated by more than a day. The mean adapted endpoint was calculated as the last 40 trials of the adaptation phase³. During adaptation trials, the peripheral contour was stepped 1° to the left and remained visible until the subject pressed a button to initiate the next trial, but during pre- and post-test trials, the peripheral contour was extinguished during the saccade. This was done to avoid extinction effects in the post-test phase that could confound a potential transfer of adaptation from the adapted saccade type.

4.2. Results

Some data were discarded because of lack of accuracy in the eye position measurement and blinks (3%), predictive or premature saccades (latency < 50 ms) (3.5%), and trials for which the endpoints were more than ± 2 standard deviations from the individual average (13.5%). Once such trials were discarded, averages for each phase and condition were calculated on about 32 observations per subject. For saccadic latency and endpoints, a 4 (Phase: Pre-test Type 1, Pre-test Type 2, Adaptation Type 2, Post-Test Type 1) \times 2 (Condition: V-saccades as Type 1, R-saccades as Type 1) univariate ANOVA was carried out. For the amount of adaptation ([pre-test endpoint—adapted or post-test endpoint]/intra-saccadic step size), a 2 (Phase: Adaptation vs. Post-test) \times 2 (Adapted saccade: V- vs. R-saccade) ANOVA was carried out. For these ANOVA, *p*-values are given in parentheses, and when indicated, *T*-tests were also performed.

4.2.1. V-saccade adaptation and R-saccade test

Saccade latencies were different ($F(1,9) = 21.4$, $p < .002$) between all gap 0 (145 ± 25 ms, no difference between pre- and post-test, $F < 1$) and all overlap trials (204 ± 42 ms, no difference between pre-test and adaptation, $F < 1$). This suggests that the two paradigms were successful at eliciting two

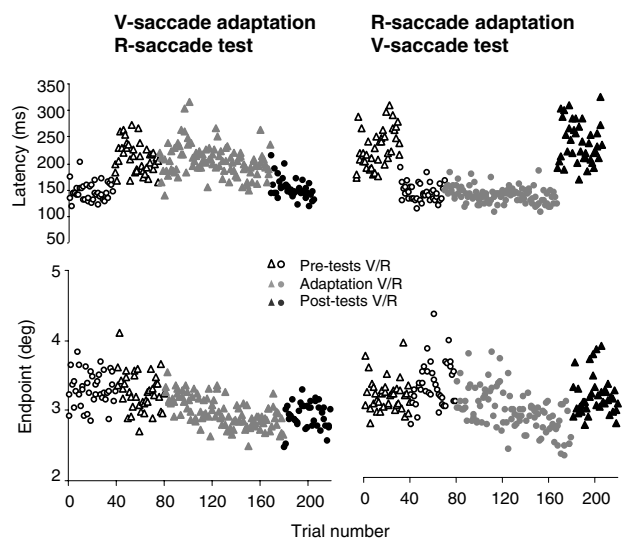


Fig. 6. Experiment 3. Saccade latencies (milliseconds) and endpoints (degrees) as a function of trial number for R- and V-saccades (circles and triangles, respectively). Left: V-saccade adaptation, R-saccade test. Right: R-saccade adaptation, V-saccade test. Open symbols: trials 1–40 and 41–80 (pre-tests). Full grey symbols: trials 81–180 (adaptation). Full black symbols: trials 181–220 (post-test). Each point is the average over the ten subjects.

different populations of saccades, with longer latencies for V-saccades than for R-saccades with overlap and gap 0 trials respectively (Fig. 6, top left). Note that the average latency in this experiment was shorter than that observed for R- and V-saccades in Experiments 1 and 2 by about 65 ms (Section 2.1.1).

The average pre-test saccade endpoint ($3.3^\circ \pm 0.5^\circ$) brought the eyes left of the peripheral contour center with no difference between R- and V-saccades ($F < 1$).⁴ This was of particular importance in assessing the transfer of adaptation, given that one of the most well defined specificities of adaptation is to amplitude (e.g. Albano, 1996). The introduction of an intra-saccadic target step caused the V-saccade endpoints to shift progressively leftward. For the first 40 trials of the adaptation phase, $10 \pm 10\%$ of V-saccades were followed by a corrective second saccade. Fig. 6 (bottom left) shows the individual endpoints for each saccade type and condition. The shift of V-saccade endpoints in the adaptation phase compensated on average for 43% of the intra-saccadic target back step ([pre-test endpoint—adapted endpoint]/step) (Fig. 7). For R-saccades, the difference between pre- and post-test endpoints was 39% of the back step. The adapted and tested saccade endpoint changes were not significantly different ($F < 1$).

³ The trials used to estimate saccade endpoint change relative to the pre-test phase differ according to saccade type (40 final trials of the adaptation phase for adapted saccades; 40 post-test trials for tested saccades). As the extinction of adaptation occurs progressively after the target stops stepping (even when reduced by the absence of visual feedback), it prevents the use of two successive post-test phases for both adapted and tested saccades. Therefore, we used a single post-test phase for tested (unadapted) saccades only. Note that the amount of adaptation may be overestimated when the final trials with a backward step are taken into account (Straube, Fuchs, Usher, & Robinson, 1997; see also Fujita et al., 2002 for a discussion on this point).

⁴ Note that the difference with Experiments 1 and 2, where the average pre-adaptation endpoint was 3.8° , results mainly from the suppression of trials in those experiments where the saccade endpoint was closer to P2 than to P4. Such a cut was done to make actual and intended saccade endpoints correspond to different DT positions. This was not necessary in Experiment 3 because subjects performed only the single saccade task. This also affects the amount of adaptation.

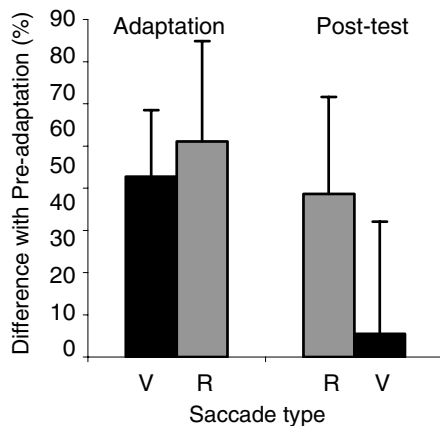


Fig. 7. Experiment 3. Average V- and R-saccade endpoint change relative to pre-test for adaptation and post-test phases. The percent endpoint change corresponds to the amount of compensation for the 1° intra-saccadic back step. Error bars are +1 between-subject SD.

4.2.2. R-saccade adaptation and V-saccade test

Saccade latencies were different ($F(1,9) = 21.4$, $p < .002$) between all overlap (232 ± 69 ms, no difference between pre- and post-test, $F < 1$) and all gap 0 trials (141 ± 20 ms, no difference between pre-test and adaptation, $F < 1$) (Fig. 6, top right). For pre-test trials, saccades landed left ($3.2^\circ \pm 0.5^\circ$) of the peripheral contour center with no difference between R- and V-saccades ($F < 1$) (Fig. 6, bottom right). The intra-saccadic target shift caused on average a 51% R-saccade adaptation (Fig. 7). For the first 40 trials of the adaptation phase, $7 \pm 9\%$ of R-saccades were followed by a corrective second saccade. The difference between pre- and post-test V-saccade endpoints (6%) was not significant ($F < 1$), and was significantly different from the R-saccade endpoint change ($F(1,9) = 22.3$, $p < .002$).

4.2.3. Asymmetric transfer profiles

The systematic backward step of the saccade target induced a similar amount of adaptation for V- and R-saccades (43% vs. 51%, $F < 1$). The difference between pre- and post-tests following the adaptation of the other saccade type was different between R- and V-saccades (39% vs. 6%, $F(1,9) = 23.1$, $p < .01$). Indeed, while the difference between R-saccade endpoints before and after V-saccade adaptation was significantly different from 0 (T -test, $p < .001$) this was not the case for V-saccade endpoints after R-saccade adaptation (T -test, $p > .10$). Intervening V-saccade adaptation (43%) caused R-saccades to shift leftward as well (39%). The R-saccade shift was 91% of the V-saccade adaptation. This ratio of the amount of endpoint change between R- and V-saccades is an estimate of the amount of transfer of adaptation to the tested saccade.

4.3. Discussion

Experiment 3 revealed an absence of transfer from R-saccade adaptation to V-saccades, and a transfer of adaptation from V-saccade adaptation to R-saccades. Such an

asymmetric transfer suggests that the gap 0 and overlap paradigms do elicit different classes of saccades.

When one compares saccade characteristics (latency and endpoints) found in this experiment (simple saccade task), with those found in Experiment 1 and 2 (dual-task), a salient latency difference appears, with shorter latencies when a simple rather than a double-task was required. As previously mentioned, the elimination of some data could also in part account for that. Nevertheless, V- and R-saccades differed in terms of latency, as expected from the different paradigms used to elicit them, and in similar proportions between the three experiments (latency of V-saccades longer than those of R-saccades by around 50–60 ms). Concerning saccade endpoints, no major differences between the experiments can be noted. In all cases, V- and R-saccade endpoints were similar and showed a rapid and progressive shift with the introduction of the intra-saccadic step (see Section 4.2.1).

The goal of Experiment 3 was to provide a stronger argument to support the claim that the overlap and gap 0 paradigms used in Experiment 1 did indeed elicit different saccade types, R- and V-, by testing the selective adaptation of one saccade type. Indeed, a symmetric and high transfer from one saccade type to the other would seriously challenge the claim that different saccades were examined. Instead, R-saccade adaptation did not transfer to V-saccades, but V-saccade adaptation transferred to R-saccades. V-saccade endpoints did not differ before and after R-saccade adaptation, concurring with previous studies that found no or only slight transfer (Deubel, 1995, 1999; Fujita et al., 2002). On the contrary, R-saccade endpoints were different before and after V-saccade adaptation, in line with previous studies (Deubel, 1995, 1999; Erkelens & Hull-eman, 1993; Fujita et al., 2002). However, the amount of transfer found here was almost complete while these previous studies reported rather a partial transfer of V-saccade adaptation to R-saccades. The causes of such a difference in the amount of transfer could reside in methodological differences between the studies. Indeed, none of these studies (including the present one) are directly comparable regarding many aspects (e.g. type and eccentricity of the saccade target; interleaving or holding constant direction and amplitude of saccades; size of target step) and particularly for V-saccades, the way they are elicited (by a tone, fixation offset or self-paced), the number of visual targets available before saccade onset (single vs. multiple) and also the subject's task (simple saccade task or combined with another task). Indeed, we believe that the high level of V-saccade adaptation transfer found here results from the paradigms used for eliciting V- and R-saccades, which differed much less from one another than in the previous studies. One could suspect that minimizing the difference between the two paradigms finally led to similar saccades types but such an argument is not compatible with the present data that also show an absence of transfer of R-saccade adaptation to V-saccades. Furthermore, a similar asymmetry of transfer was recently found with V-saccades elicited

in a scanning paradigm (Pélisson et al., 2005). The present results suggest that V-saccade adaptation takes place at a site along the programming pathway that is common to both V- and R-saccades, while R-saccade adaptation occurs at a site independent of V-saccade programming.

5. General discussion

In the present study, saccadic adaptation dissociated actual from intended EMS. The presaccadic focus of attention—indexed by discrimination performance—was found to be tied to the former as shown by the concomitant shift in the focus of attention caused by adaptation of both V- and R-saccades. The only difference between the two saccade types concerned the time course of the influence of saccade preparation on the orientation of attention, which appeared earlier for V-saccades than for R-saccades.

5.1. *The presaccadic attentional focus is oriented toward the next saccade endpoint*

When a saccade is prepared, there is a concomitant shift in visuo-spatial attention toward the position the eyes are aiming for (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). Whether the perceptual system has access to a signal representing the intended or the actual EMS (i.e. the movement required to attain the target or the movement that will actually be made) remained a question of interest. In a post-hoc analysis, Deubel and Schneider (1996) attempted to test this issue by examining discrimination performance at the intended target position and the actual saccade endpoint. When the saccade target and the DT did not coincide, there was a tendency (albeit non-significant) for better discrimination when the saccade endpoint was on the DT position (but missed the intended saccade target). Although this benefit was not as large as that associated with the intended saccade target, their results did not entirely rule out a role for the actual saccade endpoint. Furthermore, in a study where there was no precise saccade target (saccades aimed for a peripheral letter string), a spatial coupling was found between the actual saccade endpoint and perceptual performance, at the final phases of saccade preparation (Doré-Mazars et al., 2004).

The actual EMS generally coincides with the intended EMS but the systematic intrasaccadic step of the saccade target produces a change of saccade metrics resulting in a dissociation between the intended and actual EMS. The present results show that pre-saccadic visuo-spatial attention is directed toward the actual, adapted saccade endpoint rather than to the intended target position. This replicates the results of Doré-Mazars and Collins (2005) with V-saccades elicited in an overlap paradigm with an instructed saccade target, and extends them to R-saccades. Indeed, we found that the shift in discrimination performance just before saccade onset is observed whatever the intentionality of the adapted saccade (V- and R-saccades).

However, our R-saccade results are at odds with those of Ditterich et al. (2000b) who found that discrimination performance was not tied to the actual saccade endpoint and that even during back-step trials, the presaccadic attention focus remained the intended, saccadic target. In their procedure, DT was presented around 100ms before saccade onset. Several explanations could account for the discrepancy between the two studies as to the coupling between the orientation of attention and the generation of a R-saccade.

The first hypothesis is that the orientation of attention is linked to saccade preparation, for R-saccades as well as V-saccades, in particular during the last stages of motor programming. Such a hypothesis does not fit with the conclusions of Ditterich et al. (2000b). However, these authors may have failed to find a perceptual shift because they obtained weak saccadic adaptation. Indeed, the distributions for pre-adaptation and adaptation conditions overlap extensively and do not clearly differentiate distinct positions (Ditterich et al., 2000b, Fig. 4B, p. 1812). This could arise from the fact that their first 50 trials with an intrasaccadic back-step are mixed with pre-adaptation trials. As adaptation is rapid in humans, it is quite likely that for a large part of these trials, the saccades were already adapted. In this case, the absence of a perceptual shift would result not from the dissociation between saccade programming and focus of attention during adaptation, but from a failure to dissociate non-adapted from adapted saccades.

Alternatively, the distinction between the two saccade types at both behavioral (latency differences) and neurophysiological (different neural pathways) levels supports the hypothesis according to which the shift of attention related to the preparation of a saccade would differ between V- and R-saccades. Our study compared these two types of saccades directly and our results showed that, whatever the saccade type, the presaccadic attentional focus is tied to the actual saccade endpoint. One could argue that such results were found because the procedures (gap 0 and overlap) did not really elicit distinct saccade types. Several counter-arguments can be advanced. Even if R-saccade latencies were slightly longer than those usually reported, they remained shorter than those of V-saccades (50 ms difference, see Mort et al., 2003, for a discussion on this point). Moreover, in Experiment 3 the same procedure with a simple saccade task elicited V- and R-saccades with shorter latencies but where a similar latency difference persisted. Also, adaptation of R-saccades did not transfer to V-saccades, suggesting that V- and R- saccades are at least partially mediated by independent pathways that may be selectively adapted. Finally, we found differences between R- and V-saccades in the timing of the spatial coupling compatible with the idea that both saccades are generated by different pathways (see next section). A final pathway carrying EMS representing the actual, ready-to-be-executed movement would be shared by the two saccade types. Thus, the perceptual system would be informed about the consequences of the to-be-executed motor vector, whatever way the saccade was elicited.

Our findings have some theoretical implications regarding the relationship between visuo-spatial attention and saccade programming. The ‘Visual Attention Model’ (VAM; Schneider, 1995) proposed that the attentional shift precedes the eye movement and contributes to selecting the target position. The pre-motor theory of attention developed by Rizzolatti and colleagues (e.g. Rizzolatti, Riggio, Dascola, & Umiltà, 1987) claims that the shift of attention is the result of a specific eye movement program. Our results clearly argue in favor of the pre-motor theory of attention as the adaptive modification of the motor characteristics of the upcoming saccade program also shifted the position toward which visuo-spatial attention was oriented.

5.2. Differences between R- and V-saccades

The distinction of two saccade classes, R-saccades made in response to a change detected in the visual field and V-saccades directed intentionally toward permanent visual stimuli, is supported by several arguments (see Introduction). Because of these differences at the behavioral and neurophysiological levels, one might hypothesize that R- and V-saccades differ in the way the concomitant shift of attention is achieved. Our data suggest that differences arise between the two saccade types when one considers the progressive emergence of the spatial coupling between saccade endpoint and perceptual performance during saccade preparation. Best perceptual performance at the saccade endpoint emerged relatively early during the preparation of a V-saccade but only later for R-saccades. Experiment 2 allowed the elimination of the hypothesis that this difference was due to the earlier presentation of the DT in the overlap paradigm compared to the gap 0 paradigm. The interpretation of this time course difference could rely on the neurophysiological characteristics of the pathways and brain areas underlying the programming of these different saccades. Indeed, it is possible that the actual EMS we propose are used to orient attention across the visual field are delivered earlier or faster when a V-saccade is being prepared. Such a difference could be related to the higher implication of the FEF in V- relative to R-saccades. This cortical area is thought to be implied in the target selection process in V-saccade generation, because it contains neurons which respond maximally when a target lying in their receptive fields is selected for a saccade (Sato & Schall, 2003). However, if the earlier perceptual enhancement found for V-saccades is related to the selection process, one would suspect that the outcome would correspond to the intended EMS, i.e. the selected saccade target. However, in the present study the perceptual enhancement was found at the actual endpoint of the upcoming saccade. One possible explanation would be that adaptation leads to the reorganization of space perception in brain areas specifically involved in the preparation of V-saccades. During the time of saccade preparation, visual processing, target selection and motor programming are successively engaged. At the latest stage of saccade preparation (motor vector computa-

tion), processes are common whatever the pathways used to program the saccade. Perceptual enhancement of the stimuli located at the endpoint of the next saccade suggests that recurrent pathways from the saccade generator in the brainstem to cortical perceptual areas transmit actual EMS.

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