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Saccadic adaptation shifts the pre-saccadic attention focus

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Abstract The well-documented phenomenon of the spatial coupling between saccadic programming and the orienting of attention refers to the fact that visual attention is directed toward the location that the eyes are aiming for. However, the question remains open as to whether saccades and attention are two independent processes that can be directed concurrently toward a common goal, or whether their relationship is tighter, with the motor components of the saccade program influencing the selection of the position towards which visual attention is directed. To investigate this issue, an experiment was carried out in which the initial saccade goal was dissociated from the final executed motor vector. This was done by using a saccadic adaptation paradigm and a discrimination task. Results showed that best perceptual performance, which is taken to be an indicator of the locus of visual attention, followed the motor modifications arising from saccadic adaptation. This suggests that visual attention is directed toward the actual saccade landing position and that the perceptual system must have access to information regarding the motor vector before saccade execution.

Keywords Saccade · Plasticity · Perception

Introduction

Several researchers have shown that the locus of visual attention is directed toward the position aimed for by the eyes (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al 1995). For example,

when human subjects prepared a saccade to a given spatial position and performed a discrimination task on a target, best performance was achieved for targets located at the same position as the saccade goal, and performance dropped for targets located at other positions. This relative perceptual performance throughout the visual field indicates the locus of attention. Furthermore, several physiological studies have shown that activation of certain areas of the saccadic system orients attention (Moore and Fallah 2001, 2004), or that prior orienting of attention influences the direction of the upcoming saccade (Kustov and Robinson 1996). Behavioral studies have also suggested that the orientation of attention supposes the preparation of a saccade, but that the final command can be inhibited (Rizzolatti and Craighero 1998).

The exact nature of the coupling between the orienting of attention and saccade programming remains, however, to be established. Indeed, attention and saccades could be directed concurrently toward a common goal, suggesting that the two processes are independent but can be functionally and temporally coupled. The two processes could also be more tightly linked, the orientation of attention depending on the state of the oculomotor system. In order to investigate this issue, the saccade goal and the actual landing position must be distinguished experimentally, and perceptual capacities at both positions must be tested¹. This was rendered possible by combining saccadic adaptation and perceptual tasks.

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¹Deubel and Schneider (1996) found that attention was coupled with the intended saccade target rather than the actual landing position in a paradigm in which there was an obligatory saccade target. Doré-Mazars et al (2004) found that attention was coupled with the actual landing position in a paradigm with no obligatory saccade target where subjects were allowed to aim freely within the spatially extended target. Saccadic adaptation is a means of experimentally distinguishing the intended and actual saccade landing positions.

Saccades are quite precise despite the fact that their speed (250°/s) prevents visual feedback from playing any significant role in their trajectory. The gain (amplitude/target eccentricity) must therefore be calculated before saccade onset. Maintaining such precision throughout developmental and pathological changes requires mechanisms capable of evaluating errors and adapting future behavior accordingly. The progressive modification of saccadic amplitude to correct targeting errors, called saccadic adaptation, can be induced in normal subjects by the double-step procedure developed by McLaughlin (1967). It consists of shifting the saccade goal during the saccade directed toward it, producing an artificial post-saccadic targeting error. The saccade goal is thus different from the actual landing position. After several trials, the saccadic gain adapts to the intra-saccadic shift and the amplitude is modified.

Does the orientation of attention follow the adaptive shift of saccadic endpoints, or does it remain oriented toward the position of the initial, pre-saccadic goal? If attention remains oriented to the initial target position then the link between attention and saccades is the result of a concurrent orientation toward a common goal. If on the other hand saccadic adaptation is accompanied by an attentional shift then the two processes are more tightly related.

In the present experiment, subjects performed a saccade toward a peripheral visual target embedded in other patterns and a discrimination task about the orientation of a single oblique line presented just before saccade onset. For half of the trials, the visual target was shifted backward during the saccade by 1° of visual angle, in order to evoke saccadic adaptation.

Methods

Four trained naïve volunteers and one author with normal vision participated in the experiment.

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 et al 1983), with an absolute resolution of 6 arcmin and a linear output over 12°. Complete details of the eye movement recording apparatus, calibration procedure and numerical data processing can be found in Beauvillain and Beauvillain (1995). Subjects were seated 70 cm away from the screen and their heads were kept stable with a submaxillary dental print and forehead rest. The stimuli were green on a black background. The apparent luminance of the display, measured by a Minolta LS-110 luminance-meter, was 4.00 cd/m².

The visual display consisted of a foveal fixation cross and five peripheral frames (see Fig. 1A). Each frame looked like a pair of brackets [] that had been rotated by 90°, so that (what was) the left bracket was above (what was) the right bracket. The cross and

Fig. 1A–B **A** Experimental procedure. After successful calibration, the sequence of events was as follows: (1) The foveal fixation cross and five peripheral frames appeared simultaneously at 2° of eccentricity. Subjects had to maintain their eyes on the cross until (2) its offset. (3) During the preparation of the saccade, the four horizontal and vertical distracters and the single oblique target appeared for 30 ms. (4) The five frames remained empty until the end of the latency and (5) during the saccade the entire visual stimulus was shifted to the left. The frames remained empty until the end of the trial. This intra-saccadic shift occurred only on adaptation trials; on all other trials (pre-adaptation and post-adaptation phases) there was no intra-saccadic shift and the visual stimulus remained in its initial position for the entire duration of the trial. **B** Temporal dependence between adaptive landing positions shifts and perceptual shifts for (a) ST3 and (b) ST4, for the three successive phases and the three discrimination target positions (DT): DT2 (circles), DT3 (squares), DT4 (triangles). *Top panels* show landing positions, *middle panels* show saccade latency and *bottom panels* show discrimination performance, as a function of trial number. For the top and bottom panels, the x-axis represents the final trial taken into account. For example, point 12 is the average over the five subjects for the particular DT occurring in trials 1–12, point 24 is the average for the particular DT occurring in trials 13–24, and so on. In the middle panels, each point represents mean individual latencies for one trial. In the top panels, brackets on the right represent the three critical frames (2, 3 and 4)

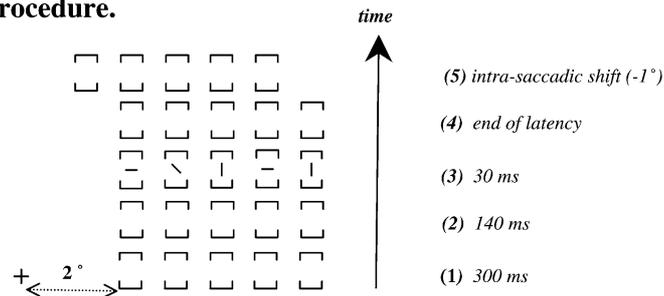
frames were presented horizontally at an eccentricity of 2° to the right. Each frame and each space between frames was 0.5° wide, so the entire stimulus took up 4.5°. The retinal eccentricity of the center of each frame, from one to five, was 135, 195, 255, 315 and 375 arcmin. During adaptation trials, the entire stimulus was shifted during the saccade by 1° to the left and remained so until the end of the trial.

Subjects had to saccade to the third (saccade target 3, ST3) or fourth frame (ST4) in separate experimental blocks, according to verbal instructions. The back-step therefore represented 24 or 19% of the initial saccade amplitude, respectively.

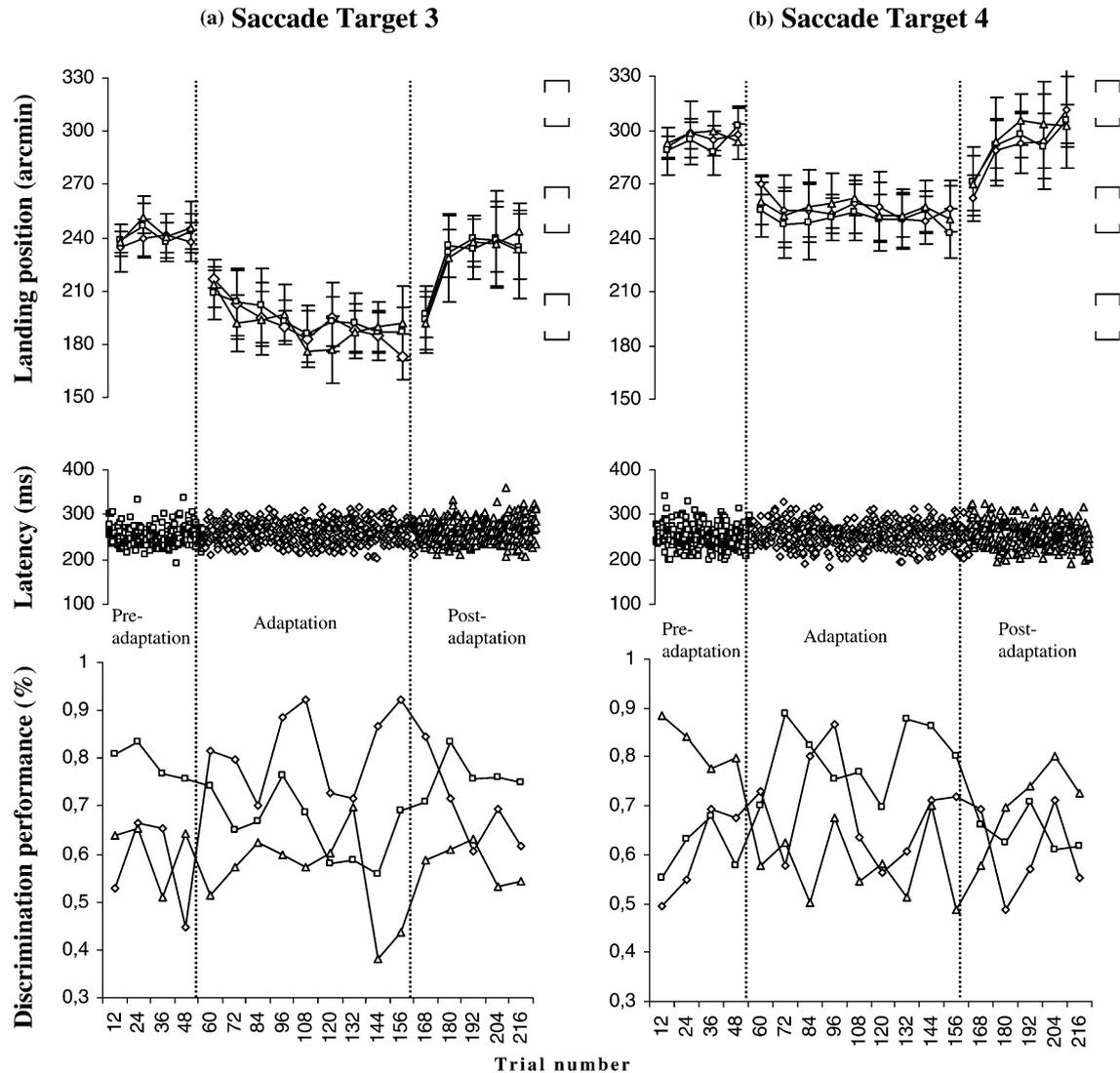
One line segment appeared in each frame during the preparation of the saccade, and could be either horizontal and vertical distracters (– and |) or the single oblique line (\ or /) (Beauvillain et al 2003). The oblique line appeared with equal probability in frames 2, 3 or 4. Subjects indicated whether the oblique leaned to the left or to the right by pressing the corresponding button placed in front of them.

The procedure was as follows (see Fig. 1A): after calibration of the eye-movement recording apparatus, the cross and peripheral frames appeared simultaneously. Subjects had to maintain fixation on the cross until its offset 300 ms later, which was the go signal for the saccade to ST3 or ST4. The 300 ms overlap between stimulus presentation and foveal offset is a classic procedure for soliciting voluntary saccades (Fischer 1986). 140 ms later, just before saccade onset, the line segments appeared in the frames for 30 ms. The frames then remained empty for the rest of the trial. The mean delay between cross offset and saccade onset (saccade latency) obtained here was 254 ms

A) Experimental procedure.



B) Temporal relationship between adaptive landing positions shifts and perceptual shifts



(± 15 ms); discrimination targets therefore appeared less than 114 ms before saccade onset. These delays are optimal for measuring pre-saccadic attention shifts (Doré-Mazars et al 2004).

For both STs, each subject took three experimental blocks containing three successive phases each. The pre-

adaptation and post-adaptation phases (the first 48 and final 60 trials) consisted of trials with no intra-saccadic shift. The adaptation phase consisted of 108 trials with an intra-saccadic shift. Trials were organized pseudo-randomly in such a fashion that each target position was tested four times (frame 2, 3 or 4) every 12 trials.

Results

Landing positions were modified by the intra-saccadic target step ($P < 0.0005$), with mean gains of 0.95 and 0.94 during the pre-adaptation phase, 0.74 and 0.80 during the adaptation phase, and 0.91 and 0.94 during the post-adaptation phase, for the two STs respectively². As can be seen in Fig. 1B (top panels), the time course of adaptation was faster, particularly for ST4, than what has usually been reported in the literature for unique STs (30–60 trials, Hopp and Fuchs 2004). This rapid adaptation might appear surprising, but several points argue in favor of an adaptive mechanism rather than a cognitive strategy. First, we observed similar saccadic latencies between pre-adaptation, adaptation and post-adaptation phases (250, 256 and 255 ms respectively, $P = 0.10$) (Fig. 1B, middle panels). Second, we believe our subjects adapted faster because, while the target was a single frame, it was presented with four other frames, and in order to aim for the correct target—ST3 or ST4—subjects had to take the position of all the frames into account, which can therefore be said to fall in the subject's attentional window. Indeed Ditterich et al (2000b) have shown that when the attentional focus includes a background that moves in the same direction as the intra-saccadic target step, adaptation is faster (slope of the linear function four times that of the function without background shift). Third, Fig. 1B (top panels) also shows that recovery was slower than adaptation. This is compatible with other reports in the literature (such as Deubel et al 1986). Asymmetric time courses for adaptation and recovery argue against rapid adaptation arising from a strategy, because in that case subjects would be expected to implement the same strategy for both adaptation and recovery.

Discrimination performance depended on the discrimination target (DT) position (frame 2, 3 or 4), saccade target (ST), and phase (pre-adaptation, adaptation, post-adaptation). An RM-ANOVA revealed a triple interaction ($P < 0.0001$) (Fig. 2). For both STs, the interaction between discrimination target position and phase was significant (both $P_s < 0.0001$), indicating that the effect of DT position varied according to the phase. Moreover, similar results were observed in pre-adaptation and post-adaptation phases, in which there was no intra-saccadic shift of stimuli: the DT was best discriminated when it appeared at the ST rather than in other frames (both $P_s < 0.005$). During the adaptation phase, the DT was best discriminated when it appeared in the frame just left of the ST (frame 2 for ST3 and

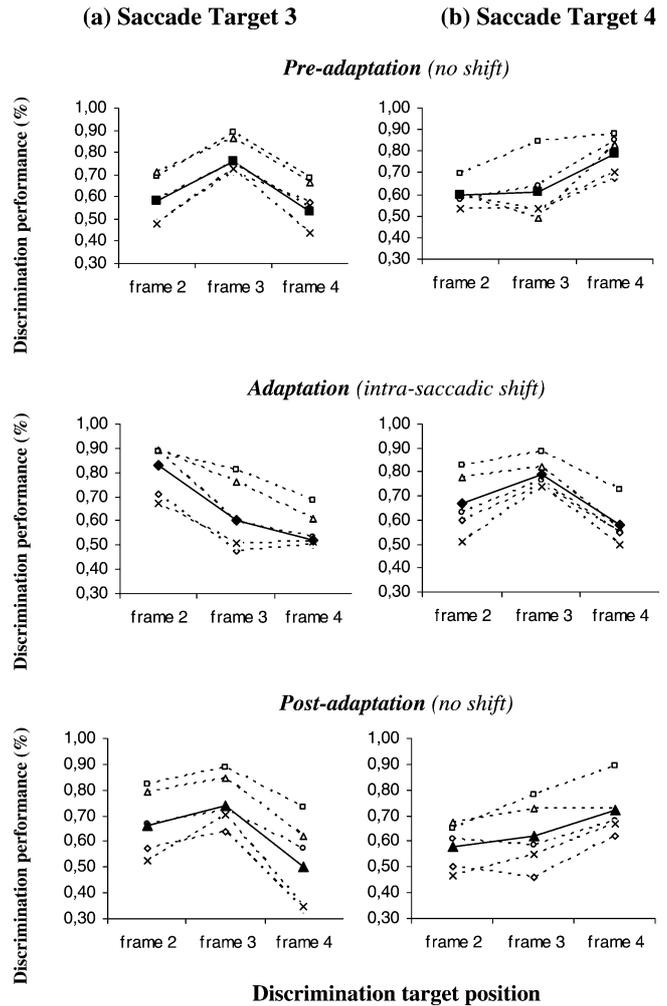


Fig. 2 Discrimination performance for (a) ST3 and (b) ST4 according to the phase (pre-adaptation, adaptation, post-adaptation) and the position of the DT (frame 2, 3 or 4). *Dashed lines* represent individual performances and *solid lines* represent average performance

frame 3 for ST4) rather than in other frames (both $P_s < 0.005$).

For each ST, best discrimination performance was associated with a DT position that corresponded to the landing position. These results suggest that discrimination performance depends on the upcoming landing position of the saccade in preparation at the moment of target presentation.

As saccadic adaptation is progressive, a temporally analog shift in discrimination performance would constitute a strong argument for a tight link between the two processes. Figure 1B (bottom panels) presents the evolution of landing positions and discrimination performance as a function of trial number.

Best discrimination performance was observed for DTs that spatially coincided with landing positions. During adaptation trials, the leftward landing position shifted quickly and the DT that was best discriminated shifted to the left as well. It seems therefore that the drop in discrimination performance for the DT at the same

²In this analysis, as well as the discrimination performance analysis below, the first 12 trials of each of the adaptation and post-adaptation phases were eliminated in order to limit the analyses to trials which clearly differentiated the three phases as far as landing positions were concerned. Time course analyses take all trials into account.

position as the ST occurred at the same time as the leftward landing position shift, at the beginning of the adaptation phase. The rise in discrimination performance for the DT at the more leftward position also occurs at this point, as the mirror image of the leftward landing position shift. Discrimination performances for the DTs that are never reached by the saccade remained weak throughout all three phases.

Discussion

The present experiment shows that the motor modifications arising from saccadic adaptation are reflected in the orientation of attention, as measured by relative perceptual performance.

During pre-adaptation and post-adaptation phases, where no intra-saccadic displacement occurred, we replicated the spatial coupling between saccade and attention found by previous studies. The intra-saccadic target displacement evoked a fast but progressive leftward shift in saccadic landing positions, as has been previously shown for complex stimuli (Ditterich et al 2000b). In this case, attention was coupled to the endpoint of the saccadic vector actually executed, taking into account adaptive modifications. The visual signal causing adaptation (Noto and Robinson 2001; Seeberger et al 2002) is available to the motor system, but our results suggest that it must also be available to the perceptual system.

The pathway leading from the superior colliculus to the frontal eye field via the mediodorsal thalamus (Lynch et al 1994; Sommer and Wurtz 1998) could carry such information to the perceptual system, since the FEF is a major center of visual selection (Schall 2004). Indeed, Sommer and Wurtz (2002, 2004a, 2004b) and Wurtz and Sommer (2004) showed that this pathway carries information allowing the motor system to take into account the perceptual consequences of eye movements in the programming of future behavior. When the brain programs a movement, it sends its motor command but also generates an internal signal (*corollary discharge*) used by sensory systems to recalibrate to the consequences of the movement. In the visual system, each saccade causes the retinal image to shift, and the colliculo-frontal pathway carries a corollary discharge signal, which could be used to compensate for these changes within the visual perception system. Indeed, Tanaka (2003) showed that when the first of a sequence of memory-guided saccades was adapted, the second saccade took the landing position shift into account and compensated its amplitude to reach the target. To do this, information regarding the first executed saccadic vector must be relayed to the saccadic system. The retinal consequences of eye movements cannot be taken into account for the programming of subsequent saccades, which as a result become inadequate when the SC-FEF pathway is cut (Sommer and Wurtz 2002). In our experiment, the presence of such recurrent information in the FEF could explain the accompanying

perceptual shift, therefore providing support for the idea that signals downstream from saccadic adaptation also influence visual perception.

Previous experiments have found perceptual consequences of saccadic adaptation with tasks other than discrimination. Adaptive shifts in landing positions influenced estimations of localization (Bahcall and Kowler 1999; Mack et al 1978) or matching direction (Moidell and Bedell 1988). Furthermore, McFadden et al (2002) found that adapting attention leads to landing position shifts. However, Ditterich et al (2000a) came to the opposite conclusion with a discrimination task, as they found that intra-saccadic shifts were not accompanied by perceptual shifts and that best performance remained tied to the pre-saccadic target position whatever the actual landing position. At least two explanations could account for the divergence between these results and our own. First, they may have failed to find a perceptual shift because they obtained weak saccadic adaptation. Indeed, the modes of the landing position distributions for “before adaptation” and “adaptation” conditions are identical and the distributions overlap extensively (Ditterich et al 2000a, Fig. 4b, p. 1812). This could arise from the fact that their first 50 trials with an intra-saccadic back-step are mixed with “before adaptation” trials. As adaptation is rapid in humans, it is quite possible that the saccades were already adapted for a large part of these trials. An alternative explanation is related to the type of saccade solicited. Indeed, while our experiment called for voluntary saccades, intentionally directed towards a permanent visual target, the paradigm used by Ditterich et al (2000a) called for targeting saccades (part of the reactive saccade class) evoked by the sudden appearance of a peripheral target. While both voluntary and reactive saccades can be adapted, it is not known whether their adaptation has the same effect on perception. Indeed, previous studies showing a tight coupling between saccade and attention all used voluntary saccades. Voluntary and reactive saccades do not depend on the same neural circuits (Pierrot-Deseilligny et al 1995), and whereas adaptation of one saccade transfers to other saccades of the same class (Hopp and Fuchs 2002), it does not transfer to the saccades of the other class (Deubel 1995). This suggests that adaptation of voluntary and reactive saccades takes place at different sites (Deubel 1999; Gancarz and Grossberg 1999). It is therefore possible that the effect of adaptation on perception is not the same for voluntary and reactive saccades.

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