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Integration of visual information for saccade production

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ABSTRACT

To foveate a visual target, subjects usually execute a primary hypometric saccade (S1) bringing the target in perifoveal vision, followed by a corrective saccade (S2) or by more than one S2. It is still debated to what extent these S2 are pre-programmed or dependent only on post-saccadic retinal error. To answer this question, we used a visually-triggered saccade task in which target position and target visibility were manipulated. In one-third of the trials, the target was slightly displaced at S1 onset (so-called double step paradigm) and was maintained until the end of S1, until the start of the first S2 or until the end of the trial. Experiments took place in two visual environments: in the dark and in a dimly lit room with a visible random square background. The results showed that S2 were less accurate for shortest target durations. The duration of post-saccadic visual integration thus appears as the main factor responsible for corrective saccade accuracy. We also found that the visual context modulates primary saccade accuracy, especially for the most hypometric subjects. These findings suggest that the saccadic system is sensitive to the visual properties of the environment and uses different strategies to maintain final gaze accuracy.

1. Introduction

Scrutinizing a scene requires numerous fast eye movements, called saccades, which shift the retinal image of objects of interest to the fovea for detailed visual analysis. When an object is located in the

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periphery of our visual field, a main saccade and (at least) a corrective one are needed to foveate it. Corrective saccades have a shorter latency than the main saccade and an amplitude of about 10% of the main saccade. The process underlying corrective saccade production is still debated in terms of its possible dependency on retinal feedback (Becker, 1976; Becker & Fuchs, 1969; Deubel, Wolf, & Hauske, 1982; Henson, 1978; Kapoula, Robinson, & Hain, 1986; Prablanc & Jeannerod, 1975; Prablanc, Masse, & Echallier, 1978). In other words, can corrective saccades be pre-programmed or do they solely depend on a retinal error signal encoded after the end of the primary saccade?

Corrective saccades have been explored by varying the time and/or location of re-appearance of the initial target. Prablanc and Jeannerod (1974, 1975) found that corrective saccades were generally absent when the visual input was turned off before the onset of the main (or primary) saccade. However, when a brief visual input was restored after saccade completion corrective saccades were elicited. Latencies and amplitudes varied according to the extent of the initial error of the primary saccade. These results seemed to contradict a previous hypothesis stating that corrective saccades were pre-programmed since their latencies were too short to allow a new computation of the target location (Becker, 1976; Becker & Fuchs, 1969). However the contradiction was only apparent as it was further shown that when primary saccades were very hypometric (gain < 0.8) secondary saccades were systematically elicited without the need of a new retinal input, and that the probability of occurrence of such internally triggered saccades decreased as the primary saccade gain increased (Prablanc et al., 1978). Deubel et al. (1982) contested Becker and Fuchs' findings in showing that corrective saccades can only occur when a stepped second target is switched on (as opposed to when no second target arises). The authors varied the time of reappearance of the target (0 ms – no target reappearance – to 60 ms after the primary saccade). They found that no corrective saccade is generated until the target reappearance, showing that retinal feedback is inherent to their generation. Other results, however, showed the retinal processing of the error during the late phase of the saccade to elicit a secondary saccade, although not fully corrective (Prablanc et al., 1978).

Eggert, Ditterich, and Straube (1999) also investigated the influence on corrective saccades of a secondary target (stepped backward or forward) occurring at different times during the primary saccade. They found that when this second target appeared during the deceleration phase of the primary saccade, the latency of corrective saccades was significantly longer than when the secondary target appeared during the acceleration phase of the primary saccade. This observation was replicated in an eye-hand coordination task where subjects had to look and point at a peripheral visual target (Gaveau et al., 2008). This suggests that corrective saccades result from a processing of the retinal signal and that intra-saccadic visual stimulus directly affects the timing of the corrective saccade, despite the well-known elevation of the visual threshold during execution of the saccade (Greenhouse & Cohn, 1991; MacAskill, Jones, & Anderson, 2003; Matin, 1974).

In most studies in the literature, the background surrounding visual targets provides no visual information, and is generally uniform or black. However, the visual environment we live in is much more complex. The role of the visual context on corrective saccades has not yet been explored. Some studies have looked at the influence of a visual background on the primary saccade, especially on saccadic adaptation (when the amplitude of the primary saccade is progressively adjusted to a systematic perturbation of target position). Ditterich, Eggert, and Straube (2000) have shown that introducing an intrasaccadic displacement of a visual background (white random dot pattern on a black screen) influences saccadic adaptation when a large target is used. According to the authors, the target size contributes to the size of the subjects' focus of attention. When its size is large enough with respect to the items of the visual background, the numerous elements of the background which fall within the attention focus are processed by the visual system. Thus, under these conditions, an intrasaccadic shift of the background can generate an error signal. Another study has shown that the visual attribute of a target could be an efficient cue to induce selective saccadic adaptation (Herman, Harwood, & Wallman, 2009). In the same session, subjects could adapt their saccades to one type of target (e.g., flickering illuminated circle) that stepped back intra-saccadically, but did not adapt saccades to another target (e.g., non-flickering illuminated circle) that remained stationary. In addition, in a control experiment, the observation of similarly adapted saccades to both types of target when the stationary target was switched off intra-saccadically suggests that processing of the visual attribute of the target as a contextual cue required post-saccadic feedback. However, these experiments have again used light

spots on dark background. White, Stritzke and Gegenfurtner (2008) have recently studied the effect of natural scenes on saccadic behavior. They found that saccade latencies were faster in the context of natural backgrounds as compared to unstructured backgrounds. All these studies suggest a possible influence of the visual context on primary saccades gain and latency, but none have addressed a possible effect on the performance of corrective saccades.

In the present study, we investigated the temporal and spatial properties of the visual stimulus required to elicit corrective saccades. The range of target amplitudes was large enough to favor the generation of secondary saccades, and targets could be randomly stepped either backward or forward in some trials. The possible effect of visual background on corrective saccade production was also tested.

Our results show that short intra-saccadic target presentations are sufficient to elicit secondary saccades, although not fully corrective, suggesting an intrasaccadic retinal error signal processing. They also show that, for the most hypometric subjects, the primary saccade gain is increased by the presence of a visual background and consequently, non-retinal secondary saccades which are frequent in these subjects, tend to be suppressed.

2. Methods

2.1. Observers

Six subjects (mean age \pm SD: 32 ± 8) participated in this study. All observers had normal or corrected to normal vision and gave written informed consent. Experiments were conducted in accordance with the Declaration of Helsinki and under the terms of local legislation.

2.2. Experimental set up and stimuli

Experiments took place in a dark room (*Dark Background* experiment) or dimly lit room with a random square pattern (126×60 cm) as a background (*Visual Background* experiment). Subjects sat in front of a 45° slanted table (see Fig. 1a). Head position and orientation were controlled with a chin rest and head restraint. An array of light-emitting diodes (LEDs, 3 mm diameter) located above a half reflecting mirror provided visual targets seen on the table surface, along a fronto-parallel line 56 cm from the eyes. Subjects saw the targets superimposed on a dark or visible background according to experiments. They were instructed to first look at a fixation target (located at 10° left from the sagittal plane) and then to shift their eyes as soon as the fixation target was replaced by a randomly presented target (three possible target locations: 12.5° , 20° or 27.5° in the right hemifield; Fig. 1b). Thus, the ocular angular displacement necessary to reach the target (target retinal eccentricity) was respectively 22.5° , 30° or 37.5° .

Horizontal eye movements were recorded with an Eye-link2 (SR Research, Canada) at a 500 Hz frequency. Eye position signals were processed on-line (differentiation with a two-point central difference derivative algorithm with a sampling interval of $1/500$ and step size of 4 ms (Bahill & McDonald, 1983)), allowing to detect the onset and end of primary and secondary saccades based on a velocity threshold (where the velocity exceeded $30^\circ/s$) and to trigger visual events (target off or target jump), as detailed below. The complete loop of processing between eye position recording and visual display changes was short, with a maximum delay of 4 ms.

2.3. Design and procedure

Each subject performed two experiments (*Dark Background* and *Visual Background*) in a counterbalanced order.

In the first experiment, each subject performed 200 trials in complete darkness (*Dark Background*); the experiment was subdivided in 2 blocks of randomized trials.

Targets could either be displaced (*Jump* condition, 36% of trials) or remain fixed at their original position (*Fix* condition, 64% of trials). In the *Jump* condition, the double-step paradigm was used to modify the error of the primary saccade: the initial target at 20° was switched to a 12.5° target

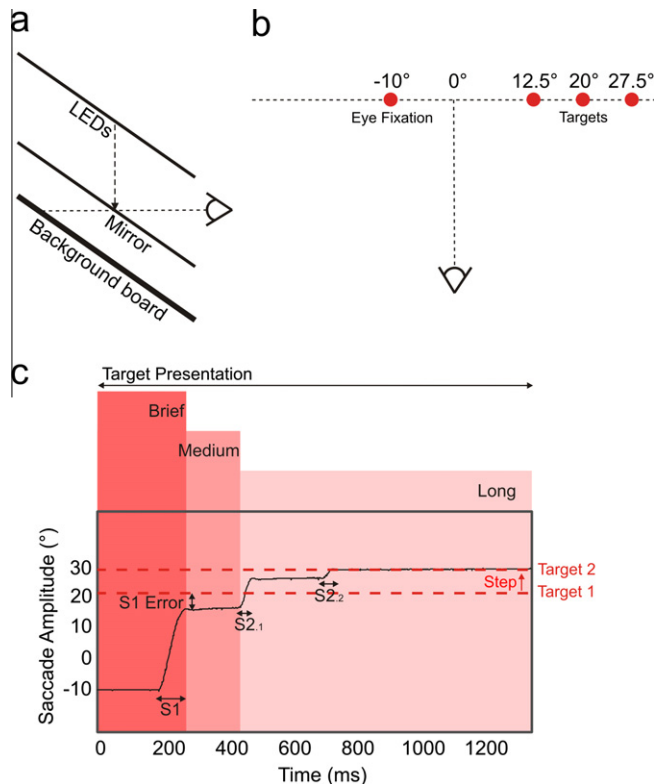


Fig. 1. Experimental set-up and procedure. (a) Side view: the LED targets were seen through a half reflecting mirror so that they appeared to the subject on the background board. (b) Locations of the LED targets with respect to the subject's trunk. (c) Duration of target jump. Individual saccadic trace (black) for a target jumping from 30 to 37.5° at S1 saccade onset. Target jump could be *brief* (turned off at S1 end), *medium* (turned off at S2.1 saccade onset) or *long* (target visible until end of trial). Note that depending on subjects (hypometric subjects), additional S2 (S2.2) could be performed.

(*Backward* condition) or to a 27.5° target (*Forward* condition) at saccade onset. Among these *Jump* trials, the timing of target presentation was randomly varied to investigate the visual target information processing: the target was maintained either until the end of the primary saccade S1 (*Brief* timing), until the start of the first secondary saccade S2.1 (*Medium* timing), or until the end of the trial (*Long* timing) (see Fig. 1c). All conditions described above were randomized to avoid subject's anticipation or any saccadic adaptation.

A second experiment replicated the first one with an added *Visual Background* (a square wave random pattern (made of 3 mm black and white squares) filling the entire experimental field) in order to determine the visual requirements for corrective saccade production by decreasing the detectability of the target and the intrasaccadic target jump¹. All conditions cited above are summarized in Table 1.

2.4. Off-line data analysis

The horizontal eye position signal was first filtered (finite impulse response filter FIR, 50 Hz cut-off frequency) and eye velocity was computed from the filtered position signal. The sequence of eye

¹ The background was applied on the dimly lit device panel (as opposed to the first experiment, with a dark panel in a completely dark room). All subjects indicated that all targets (including intrasaccadic target jumps) were more difficult to detect in this condition.

Table 1

Summary of all conditions used in the study. The same conditions are used for *Dark* and *Visual Backgrounds*.

		Fix	Backward jump	Forward jump
Dark background	Target duration	Long	Long, medium, brief	
	Target eccentricity	22.5°, 30°, 37.5°	30°→22.5°	30°→37.5°
Visual background	Target duration	Long	Long, medium, brief	
	Target eccentricity	22.5°, 30°, 37.5°	30°→22.5°	30°→37.5°

movements was defined by detecting automatically the beginning and the end of the primary and corrective saccades based on a 30°/s velocity threshold. The results of this automatic procedure were then inspected and corrected manually, if necessary. Several saccade-related parameters were computed: for *Fix* condition, the primary saccade S1 error and the first secondary saccade S2.1 error were calculated as the difference between target position and eye position at the termination of S1 and S2.1, respectively. For *Jump* condition, the final target location (Target 2) was used to compute the saccadic errors for S2.1, whereas for S1 two different error parameters relative to initial and final target locations were computed (S1 error relative to Target 1 and to Target 2, respectively). For all conditions, S1 reaction time (RT) relative to target onset, S2.1 reaction time relative to S1 offset and the number of S2 were also evaluated. Final eye position error and the corresponding time of final capture were computed at the end of the last S2. Finally, the effect of each condition on S1 and S2.1 accuracy (timing of target presentation, jump or fix condition, and visual background) was assessed with separate repeated-measures ANOVA carried out on all subjects (Statistica v. 8.0, StatSoft).

3. Results

3.1. General overview

As a control condition, targets remained stationary at their original position (*Fix* condition). As expected, *Fix* condition leads to the best accuracy of final eye position (mean final error = -0.09° , ± 0.05) as compared to *Jump* condition (when targets are displaced) (Fig. 2a), with shortest S2.1 reaction time (Fig. 2b). No significant difference was observed for S1 error relative to the original target (Target 1) as compared to *Jump* condition ($F(1, 5) = 0.43$, $p = .7$, Fig. 3a). The final error was independent of the background (*Visual* or *Dark*, $F(1, 5) = 0.56$, $p = .48$, and Fig. 3b, left column). However, a significant difference for S1 accuracy was found between both backgrounds ($F(1, 5) = 9.5$, $p < .05$; Fig. 3a), as well as for final capture time (saccade completion, $F(1, 5) = 8$, $p < .05$; Fig. 3c) and the mean S2 number ($F(1, 5) = 7.3$, $p < .05$; Fig. 4a).

In general, a significant interaction appeared between *Jump* and *Target duration* conditions for the final error, $F(2, 10) = 81$, $p < .0001$, but not for time of final capture, nor for the mean S2 number and the S2.1 reaction time ($F(2, 10) = 3.3$, $p = .7$; $F(2, 10) = 3.6$, $p = .06$; $F(2, 10) = 1.3$, $p = .3$, respectively). A strong significant interaction has been observed between *Background* and *Jump* conditions for all eye parameters (final error $F(1, 5) = 21$, $p < .005$; capture time $F(1, 5) = 7.5$, $p < .05$; S2 number $F(1, 5) = 10.9$, $p < .05$; S2.1 reaction time $F(1, 5) = 8.5$, $p < .05$; Figs. 3 and 4 (medium and right columns)). However, the *Background* condition interacted with *Target duration* only for final error, $F(2, 10) = 31.3$, $p < .001$. Detailed analyses are found in the following paragraphs.

3.2. Jump condition

3.2.1. Target duration effect

In both *Dark* and *Visual Background* experiments, each new target position (after target jump) was either lit until the end of the primary saccade S1 (*Brief* timing), until the start of the first secondary saccade S2 (*Medium* timing), or until the end of the trial (*Long* timing). A main effect of target duration was found for final error and for corresponding time of final capture, $F(2, 10) = 45.8$, $p < .0001$, and $F(2, 10) = 11.9$, $p < .005$, respectively. *Long* and *Medium* timings revealed similar final error (-0.41° , ± 0.1

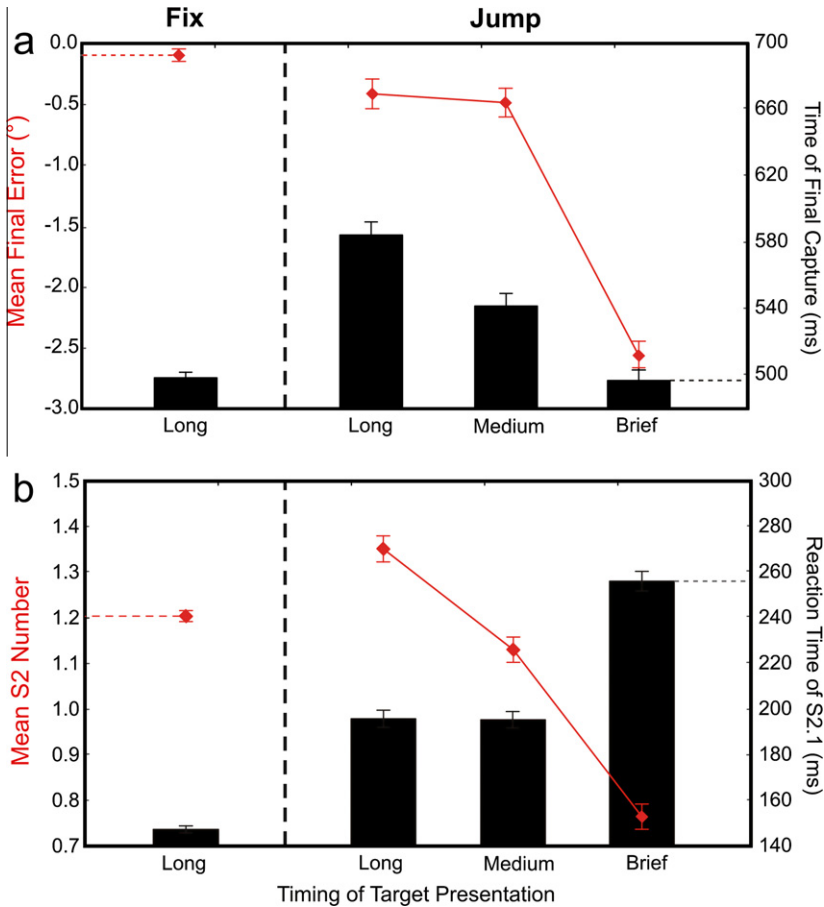


Fig. 2. Effect of target jump and of timing of target presentation on saccadic performance. Data pooled over all subjects and target eccentricities. For the *Jump* condition (right panel), the responses for the three timings (*Long*, *Medium* and *Brief*) are plotted separately. (a) Saccadic final error in degrees ($M \pm SD$, red diamonds, left scale) and time of saccadic final capture in ms ($M \pm SD$, bars, right scale). (b) Total number of S2 per trial ($M \pm SD$, red diamonds, left scale) and reaction time of the first S2 (S2.1) in ms ($M \pm SD$, bars, right scale).

and -0.48° , ± 0.1 , respectively) (Fig. 2a), whereas *Brief* timing showed the worst accuracy of all conditions (-2.6° , ± 0.2).

The time of final capture for *Long* timing increases compared to *Medium* timing (584 ms, ± 7.8 and 541 ms, ± 7.5 , respectively): this effect can be accounted for by the number of S2 in *Long* timing (Fig. 2b) that is higher than in *Medium* and *Brief* timings (1.3, ± 0.02 , 1.1, ± 0.02 and 0.7, ± 0.02 respectively). Interestingly, *Medium* timing lead to similar final eye position accuracy as compared with *Long* timing but quicker, e.g., with less S2 number. For *Brief* timing, final eye position inaccuracy was paired with a longer S2.1 reaction time and a lower number of corrective saccades. These differences are indeed revealed by a main effect of target duration on both S2 number and S2.1 latency, $F(2,10) = 72.2$, $p < .0001$, and $F(2, 10) = 39.9$, $p < .0001$, respectively. A main effect of duration was also found for S2.1 accuracy, $F(2, 10) = 11.6$, $p < .001$. As expected, no significant effect was observed on the primary saccade S1 accuracy (S1 error; $F(2, 10) = 0.06$, $p = .94$) and latency ($F(1, 5) = 0.4$, $p = .67$); Fig. 3a).

Thus, the jumped target has to be present at least during the inter-saccadic delay between S1 and S2.1 in order to be accurately foveated. When absent during the inter-saccadic delay (i.e., turned off at the end of S1), final eye position accuracy decreases.

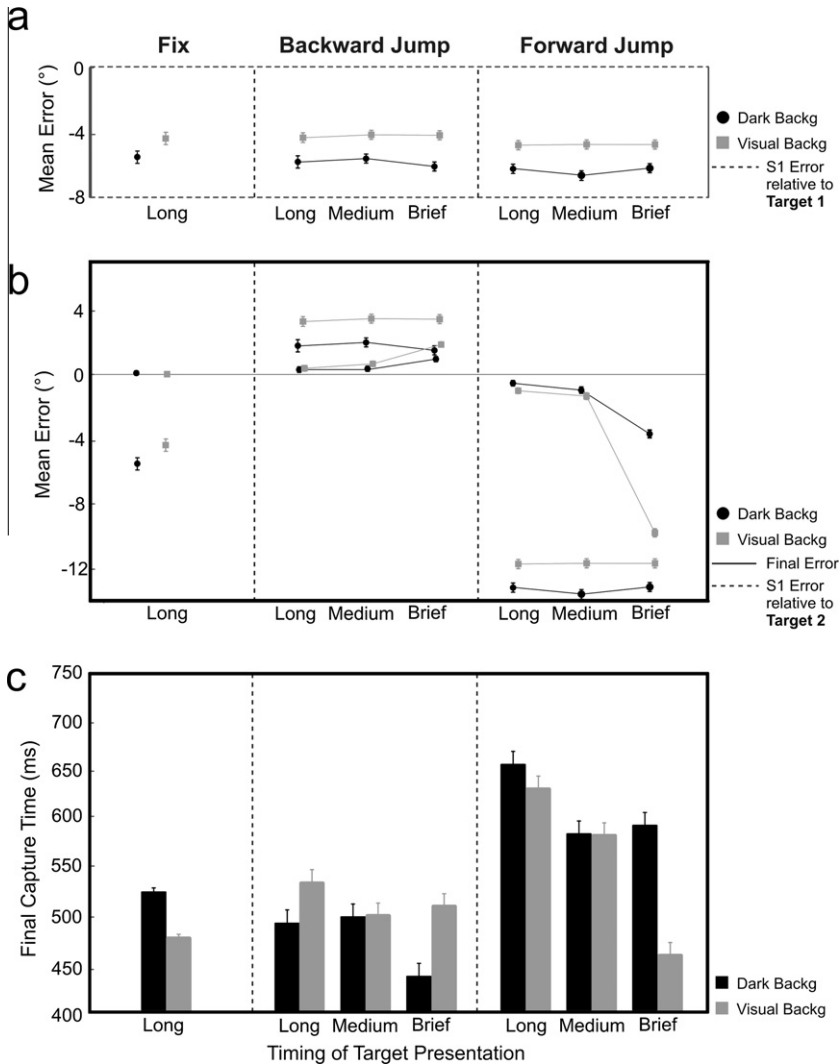


Fig. 3. Effect on S1 and final saccadic performances of *Jump* condition (*Fix* (no jump), *Backward* and *Forward* jumps), of timing of target presentation (*Long*, *Medium* and *Brief* timings) and of background (*Dark* or *Visual Background*). Data pooled over all subjects and target eccentricities. (a) S1 error relative to target 1 in degrees (Mean \pm SD) for *Dark Background* (Filled dark circles) and *Visual Background* (Filled gray squares). (b) S1 error relative to target 2 (dashed lines) and final error (solid lines) in degrees (Mean \pm SD) plotted for *Dark Background* (Filled dark circles) and *Visual Background* (Filled gray squares). (c) Time of final capture in ms (Mean \pm SD) for *Dark Background* (Dark bars) and *Visual Background* (Gray bars).

3.2.2. Jump effect

Targets could either jump on the left (*Backward* jump) or on the right (*Forward* jump). A main effect of this jump direction factor was found for final error, $F(1, 5) = 175.6, p < .0001$, and for final capture time, $F(1, 5) = 35.2, p < .005$. As shown in Fig. 3b, mean final error is close to 0° in *Backward* condition ($0.57^\circ, \pm 0.2$, center column) while it increases in *Forward* condition ($-2.88^\circ, \pm 0.5$, right column). This mean difference is especially clear in 'Brief' trials, as illustrated by a significant interaction between the jump direction and the target duration factors, $F(2, 10) = 81.9, p < .0001$. No interaction was found for the time of final capture ($F(1, 5) = 3.4, p = .08$, see also Fig. 3c). The difference of final error between *Backward* and *Forward* is essentially due to S1 error as primary saccades are generally hypometric.

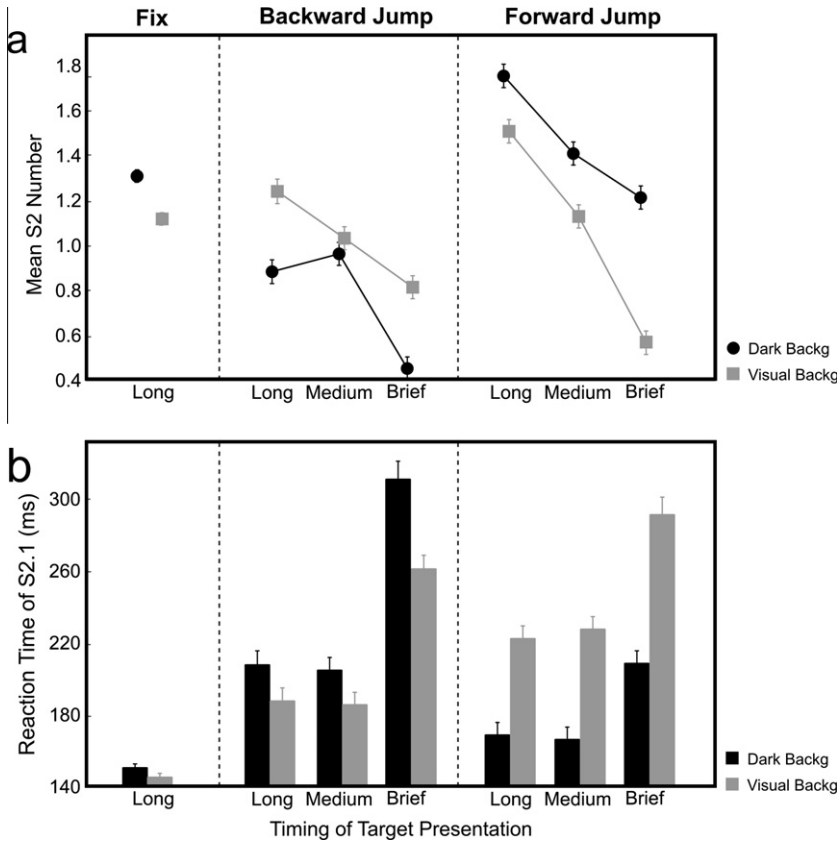


Fig. 4. Effect on S2 performances of *Jump* condition (*Fix* (no jump), *Backward* and *Forward* jumps), of timing of target presentation (*Long*, *Medium* and *Brief* timings) and of background (*Dark* or *Visual Background*). Data pooled over all subjects and target eccentricities. (a) Total number of secondary saccades (S2) per trial (Mean \pm SD) for *Dark Background* (Filled dark circles) and *Visual Background* (Filled gray squares). (b) First secondary saccade (S2.1) reaction time in ms (Mean \pm SD) for *Dark Background* (Dark bars) and *Visual Background* (Gray bars).

Thus, S1 error relative to target 2 (S1/T2) is smaller in *Backward* condition as compared to *Forward* condition (see Fig. 3b, medium versus right panel). This weaker S1/T2 error in *Backward* condition also entails less corrective saccades (see below).

Final error significantly increased for *Brief* timing in *Backward* condition (0.7° , ± 0.15), and dramatically decreased in *Forward* condition ($-6.5^\circ \pm 0.25$). A significant difference in time of final capture was found between *Backward* and *Forward* conditions ($498 \text{ ms} \pm 47$ and $591 \text{ ms} \pm 40$, respectively) that can be mainly explained by the number of S2 needed to complete the response (Fig. 4a). Indeed, a main effect of jump was found for the number of S2, $F(1, 5) = 24.3$, $p < .005$, that significantly increased in *Forward* condition compared with *Backward* condition (1.25 ± 0.15 and 0.9 ± 0.1 , respectively). A main effect of jump was also found for S2.1 error, $F(1, 5) = 59.2$, $p < .001$, in *Backward* condition, 93% of S2.1 was defined as corrective (i.e., generated toward the target location) compared to 63% in *Forward* condition. This difference is essentially due to the fact that hypometric S1 brought the eyes closer to the *Backward* target, as explained above. No significant main effect of jump was observed for S2.1 latencies ($F(1, 5) = 0.48$, $p = .52$).

3.2.3. Effect of background

One experiment took place in a completely dark environment (*Dark Background*), whereas the other experiment was performed in presence of a random-squares background (*Visual Background*). A main

effect of the *Background* condition was found for S1/T1 error, $F(1, 5) = 87.7, p < .05$, and for final error $F(1, 5) = 17.3, p < .01$. This effect can be observed in Fig. 3a, where S1/T1 errors for *Visual* condition are systematically lower as compared with *Dark* condition. Considering now S1 error relative to the (jumped) target 2, the effect of the *Visual Background* is detrimental in *Backward* condition but beneficial in *Forward* condition. Here again this difference between *Backward* and *Forward* may be explained by S1 natural hypometry, which appeared to be slightly reduced by the visual background relative to the dark environment. No significant effect was found for other saccadic parameters (time of final capture, S2 number, S2.1 latency and S1 latency).

The *Background* condition also interacts with target duration, $F(2, 10) = 31.3, p < .0001$; final error increases with *Brief* timing, $F(2, 10) = 21.3, p < .01$, and further increases for *Visual Background* ($-3.6^\circ, \pm 0.5$ and $-9.2^\circ, \pm 0.8$, respectively; Fig. 3b middle and right panels).

A significant interaction between *Background* and *Jump* conditions was found for time of final capture, $F(1, 5) = 7.5, p < .05$ (Fig. 3c). This interaction could be explained by the number of S2 (Fig. 4a) that is significantly lower for *Dark Background* in *Backward* condition and higher in *Forward* condition, $F(1, 5) = 10.9, p < .05$. More precisely, the number of corrective saccades S2.1 slightly decreases according to the background for *Backward* condition (96% in *Dark*, 90% in *Visual* condition) while it dramatically increases in *Forward* condition (56% in *Dark*, 71% in *Visual* condition). A significant effect of the background was also found for all jump conditions for S2.1 error, $F(1, 5) = 19.8, p < .001$ (75% in *Dark* condition, 82% in *Visual* condition). Note that a significant interaction between *Jump* and *Background* was also found for S2.1 latencies, $F(1, 5) = 8.5, p < .05$ (Fig. 4b).

These effects show again that, as seen in *Brief* timing, final error could largely increase, and more so when visual target position can be hardly extracted due to the presence of the random-squares background (under *Visual Background*).

3.3. Fix condition

3.3.1. Effect of background and target position

A main effect of target eccentricity ($22.5^\circ, 30^\circ$ or 37°) was found on final eye position accuracy, $F(2, 10) = 5.6, p < .05$. Surprisingly, an effect of background was found for time of final capture, $F(1, 5) = 21.9, p < .01$. Indeed, *Dark Background* led to a longer final capture compared to *Visual Background*: this difference in time was due to an increase of S2 number ($1.35, \pm 0.016$ in *Dark*, versus $1.1, \pm 0.016$ for *Visual* condition, Fig. 4a). An effect of the background and target position was also found for S2.1 error, $F(2, 10) = 4, p < .01$. Corrective S2.1 were less frequent (70%) in *Dark* condition than in *Visual* condition (87%). As S1 endpoints were farther from target positions in *Dark* than in *Visual* condition, additional S2 had to be performed.

For the *Dark* condition, the number of S2 varied between subjects, $F(10, 1508) = 57.9, p < .0001$ (one-way between subjects ANOVA) and was correlated with their S1 hypometry. This can be seen in Fig. 5a and c where subjects are ranked from the most hypometric (VG) to the less one (LU). For comparable final eye position accuracies, highly hypometric subjects (VG, OS) often executed more than one S2 with short S2.1 latencies (Fig. 5b(up) and c), while the less hypometric subjects (such as LJ or LU) rarely produced more than one S2, and S2.1 latencies were long. Surprisingly, when a *Visual Background* was introduced, subjects' behavior tended to be more homogeneous, with a reduction of S2 numbers for hypometric subjects (especially for target eccentricities at 22.5° and 30° , Fig. 5c), an increased of S2.1 latencies (Fig. 5b(down)) and a decreased S2.1 error for subjects VG and OS at all target eccentricities, as well as PE at 30° of eccentricity. S1 accuracy varied according to subjects and *Background* condition, $F(5, 1502) = 9, p < .001$, with a decreased error for target eccentricities at 30° and 37.5° in *Visual* condition (Fig. 5a) for all subjects except VG at 37.5° . Finally, no effect of *Background* nor *Target eccentricity* was found for S1 latencies, $F(1, 5) = 0.13, p = .72$, and $F(2, 10) = 8, p = .07$, respectively.

4. Discussion

Our results have shown that the presence of the target immediately after S1 completion has a major effect on final error.

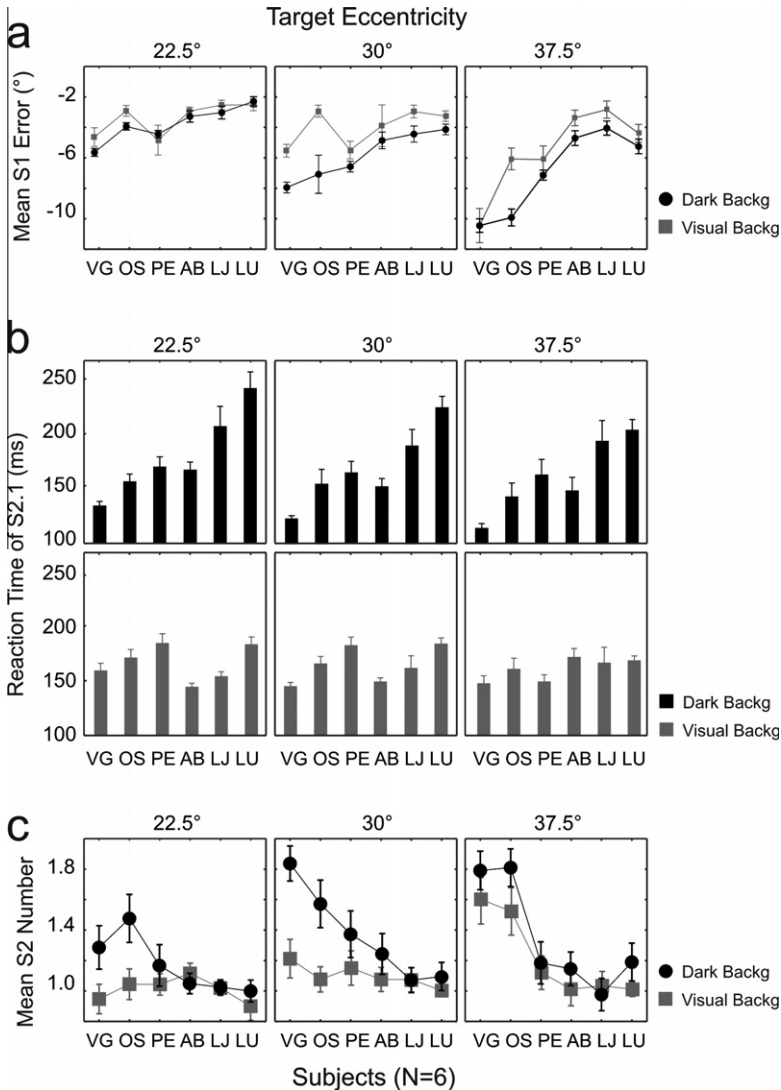


Fig. 5. S1 and S2 saccadic performances for *Fixed* condition and for each target eccentricity (Left column: 22.5°, middle column: 30° and right column: 37.5°) plotted separately for each subject (subjects ordered from the most to the less hypometric). (a) Primary saccades (S1) error in degrees (Mean \pm SD) for *Dark Background* (Filled circles) and *Visual Background* (Filled squares). (b) First secondary saccade (S2.1) reaction time in ms (Mean \pm SD). Results for *Dark Background* (upper panel) and for *Visual Background* (lower panel). (c) Total number of secondary saccades (S2) per trial (Mean \pm SD).

First, the increased final eye accuracy in the medium target condition, as compared to the brief condition, is related to an increased number of secondary saccades S2. A faster initiation (shorter latency) of the first secondary saccade S2.1 was also observed in the *Medium* timing condition. These results confirm other studies suggesting a major role of visual feedback in the production of accurate secondary saccade (Eggert et al., 1999; Munuera, Morel, Duhamel, & Deneve, 2009; Prablanc et al., 1978).

Second, the trend toward hypometry of primary saccade S1 largely explains the various effects of *Backward* and *Forward* conditions. Indeed, the S1 hypometric error was increased by the target jump in the *Forward* condition, whereas it was decreased and even inverted in the *Backward* condition.

Third, the introduction of a noise in the *Visual Background* resulted in an increased gain of the primary saccade S1 (and therefore a decrease of its hypometric trend), all the more pronounced as the subjects were more hypometric in darkness. As a consequence, the post-saccadic retinal error was increased by the *Visual Background* in the *Backward* condition and decreased in the *Forward* condition. Accordingly, the *Visual Background* also increased the number of S2 and decreased the S2.1 latency in the *Backward* condition, and led to symmetric changes in the *Forward* condition.

Fourth, the effect of the *Visual Background* was to normalize the reaction time of the first secondary saccade among subjects: indeed, in darkness, the more hypometric subjects were, the shorter the latency of their first secondary saccade, whereas with a visual background, the latency of the first secondary saccade tended to become homogenous among subjects.

To our knowledge, the present study provides the first evidence of a visual background influence on the gain of primary reactive saccades. This interesting finding opens a new opportunity to examine saccade behavior in a more complex visual environment in order to determine the contribution of multiples sources of relevant information to saccade generation.

4.1. Timing of saccade error correction mechanisms

Our results have shown that corrective saccades depend on post-saccadic retinal error. These results do not favor a strict pre-programming hypothesis, because both the number and accuracy of secondary saccades increase in the medium condition as compared to the brief condition. Furthermore, when the post-saccadic retinal information is present until the execution of the first S2 (medium condition), the final eye position is as accurate as when the target remains visible until the end of the trial (long condition). These findings reinforce previous works supporting the assumption that corrective saccades mostly depend on a retinal error signal (Deubel et al., 1982; Eggert et al., 1999; Prablanc & Jeannerod, 1974; Prablanc et al., 1978). This is compatible with recent evidence that subjects rely more on visual feedback than on extraretinal signals to generate accurate saccadic corrections in a double step task (Munuera et al., 2009). However, as our experiment in the *Dark Background* condition revealed a large inter-subject range of primary saccade gain, our data are also compatible with some apparently divergent results and interpretations of the exogenous or endogenous origin of the first secondary saccade (Becker, 1976; Becker & Fuchs, 1969; Shebilske, 1976). Indeed we observed that when the primary saccade was very hypometric, the large error signal between the short-term target location memory and the saccade efference copy was sufficient to elicit a non-retinal secondary saccade.

4.2. Effect of visual background on saccade generation and correction mechanisms

Our results also suggest that saccadic behavior varies according to visual properties of the background. Paradoxically, the presence of a visual background which seemed to reduce target detectability led to an increased final accuracy mainly through a less hypometric primary saccade, irrespective of the jump condition. Note further that, as already mentioned in the previous paragraph, the presence of a visual background has a detrimental effect on the intra-saccadic processing of target location, as expressed by final error in brief stimulus condition. Thus, the visual background may have improved the peripheral processing of static visual signals for S1 planning but at the same time degraded the peri-foveal processing of dynamic (during S1) visual signals to prepare S2.

For stationary targets (fix condition), the presence of a visual background had a beneficial effect on the primary saccade S1. Indeed, as compared to the dark condition, the error at the end of S1 was reduced in the *Visual Background* condition. A beneficial effect of *Visual Background* was also noted for the final capture time, an effect which can be related both to a smaller number of secondary saccades and to their slightly smaller reaction time.

As concern the inter-individual variability under the dark condition, the number of S2 was greater for the most hypometric subjects, whereas their S2.1 latencies were smaller, as compared to the corresponding measures for the less hypometric subjects. This observation is in agreement with the known inverse relationship between the latency of S2.1 corrective saccades and their amplitude

(Becker, 1972). The global effect of the visual background was to homogenize S2.1 latencies between subjects and to equalize the number of secondary saccades for moderate eccentricities.

White et al. (2008) have shown that S1 latency was faster in response to a target presented in a structured or natural background than in a uniform background, when target visibility was matched between background conditions. The authors concluded that the saccadic system compensates for the masking created by structured backgrounds. In our study, we did not find any S1 latency difference, but the following reasons may explain this difference with White et al.'s findings. First, although no detection task was performed, our constant intensity targets presumably had a lower visibility under *Visual Background* as compared to *Dark*. It is only when targets visibility was matched (following a detection task performed by the same subjects) that White et al. found faster S1 latencies in the structured background conditions. Second, the fact that White et al. did not report any difference in S1 amplitude could be related to the smaller eccentricity (8°) they used as compared to ours (22.5° to 37.5°). Beutter, Eckstein, and Stone (2003) have already shown that saccades and perception are similarly affected by target contrast. The accuracy of peri-saccadic localization depends on stimulus visibility: indeed, both low luminance stimuli and low contrast stimuli are more mislocalized (Georg, Hamker, & Lappe, 2008). A third explanation could be the role of attention. Ditterich and colleagues (2000) have tested subjects in detection tasks with two different types of stimuli: one foveal cross target and one circle target much larger than the cross. As subjects' reaction time was smaller with the large circle target, they suggested that subjects' attention was not spatially restricted but widely distributed. In the same vein, Harwood, Madelain, Krauzlis, and Wallman (2008) have shown that the attended region rather than the target size modulates saccadic latencies. In our study with constant size targets, a possible interpretation of the lack of modulation of the saccade latency by the *Visual Background* is the following. The increased level of subjects' attention led to a trend toward shorter latency of the primary saccade, but at the same time the decreased detectability of the targets from the background led to a trend toward longer latency. These opposite trends may have resulted in the observed similar latency of the primary saccade as in the *Dark Background*, but with a higher accuracy.

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