Research Report

Saccadic adaptation depends on object selection: Evidence from between- and within-object saccadic eye movements

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ABSTRACT

The accuracy of saccadic eye movements is maintained by saccadic adaptation. Post-saccadic visual feedback about the error between the target position and the saccade endpoint is crucial to the adaptive process. The present experiments examine the adaptation of saccades that select a new target object (between-object saccades) and that of saccades that would not aim for a selected target but execute a fixed motor vector (within-object saccades). We show that the post-saccadic visual error, induced by the intra-saccadic back step, leads to the adaptation of between-object saccades but not of within-object saccades. Furthermore, between-object saccade adaptation does not transfer to within-object saccades. These results suggest that saccadic adaptation depends on the selection of a precise target object.

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1. Introduction

Saccadic adaptation is the progressive correction of saccade targeting errors that ensures the accuracy of future behavior. Adaptation can be observed in patients recovering from dysmetria after extra-ocular muscle damage (Abel et al., 1978) or in healthy subjects after systematically displacing the target during the saccade directed towards it (McLaughlin, 1967; Deubel et al., 1986). Adaptation depends on visual feedback about the error between the visual target and the saccade endpoint (Noto and Robinson, 2001). Visual error information is crucial to saccadic adaptation because adaptation depends on the physical and temporal characteristics of the error (Bahcall and Kowler, 2000; Shafer et al., 2000). The goal of most eye movements is to bring a new object of interest onto the fovea, however a large number of saccades explore the same object. Indeed, analyses of eye movement patterns in the scanning of natural visual scenes reveal that subjects make a great number of small saccades, and a large number remain in the vicinity of or within the same object (e.g., Melcher and Kowler, 2001). It has been suggested that such within-object saccades do not aim for a specific target position, as between-object saccades do, but rather execute a motor vector of fixed size (e.g., Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006). We hypothesize that because within-object saccades do not aim for a selected target, if saccadic adaptation requires the selection of a visual target, then within-object saccades should not adapt in the same way as between-object saccades do. The goal of the present experiments was thus to investigate whether visual target selection is necessary for saccadic adaptation to take place. To do this, we examined the capability of both between-and within-object saccades to adapt to a systematic intra-saccadic shift of the visual configuration.

Eye movements can be classified according to numerous criteria but we focus here on the type of action planned on a
visual object: to aim for it (between-object saccades) or to explore it (within-object saccades). Between-object saccades have been extensively studied. Research on oculomotor control usually places subjects in a situation where only a single or a few visual targets are available. The target is usually small (a point or cross) and sensory–motor transformation, i.e. the conversion of spatial information about visual object location into motor commands, depends on establishing a simple correspondence between visual and motor coordinate systems. Thus, a visual stimulation at a given retinal position gives rise to a motor command of appropriate direction and amplitude. If a single point is the traditional laboratory stimulus, the vast majority of objects in natural environments are spatially extended. When such a stimulus is selected by the saccadic system, the eyes generally land near its center, suggesting that the representation of a central reference position within the spatially extended stimulus is used to guide saccades (Kowler and Blaser, 1995). Within-object saccades are much less studied, except in reading studies that have established the preponderant role of word size on the probability of making more than one fixation on words (e.g. McConkie et al., 1989). Even if a debate exists about the moment the within-word saccade is coded, its amplitude increases with word length suggesting that object size is crucial for within-object saccades.

While between-object saccades aim for a specific position in the selected object (i.e. its center), previous research has shown that within-object saccades are coded as a motor vector of fixed magnitude applied whatever the previous saccade endpoint in the object (Vergilino and Beauvillain, 2001; Beauvillain et al., 2005). Such a hypothesis comes from studies that introduced saccade targeting errors by eye movement contingent displacement during the first saccade directed toward one or two objects defined by the spatial grouping of elements. When the subsequent saccade was a between-object saccade, the errors were corrected in order to maintain accuracy, but when it was a within-object saccade, no such correction was found, and the first saccade endpoint error was propagated on the second saccade endpoint (Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006). In this case, the amplitude of the second saccade was constant and based on the object size integrated before the first saccade (Vergilino and Beauvillain, 2000). Moreover, whereas the saccadic system also compensates for first saccade endpoint changes resulting from saccadic adaptation to maintain accuracy of subsequent between-object saccades, it does not when the subsequent saccade explores the same object (Doré-Mazars et al., 2006).

In the present study, we examined whether saccadic adaptation depended on object selection by comparing within- and between-object saccades. To our knowledge, saccadic adaptation has been studied only with between-object saccades. We asked subjects to scan one long or two short peripheral objects occupying the same visual space (one long X-string or two short X-strings, see Fig. 7B). Most of the time, subjects scanned the visual configuration with two saccades. In Experiment 1, we attempted to directly adapt the second saccade of the sequence by introducing a systematic backward step of the entire visual configuration during the second saccade execution. Within- and between-object saccades were tested in separated blocks. In Experiment 2, we attempted to indirectly adapt the second saccade of the sequence by using adaptation transfer. Subjects were required to make two successive saccades towards two isolated crosses, and the second saccade was adapted by introducing a systematic intra-saccadic backward shift of the second isolated target (IT). Interleaved with such trials, object conditions similar to Experiment 1 were presented, but the second saccade was memory-guided. If adaptation transfer does not depend on the selection of a target object, we expect the second saccade adaptation to transfer to both second saccade types (between- and within-object saccades) because they are all volitional rightward saccades with similar amplitudes. Indeed, adaptation of volitional visually guided saccades transfers to memory-guided saccades (Deubel, 1995; Fujita et al., 2002). If transfer does depend on the selection of a target object, adaptation is expected to transfer to the second saccades in the two-object condition because both belong to the between-object saccade class but no transfer is expected to within-object saccades despite metrical similarities with the adapted saccade.

2. Experiment 1: selective second saccade adaptation

In the first experiment, we attempted to directly adapt the second saccade of a two-saccade sequence directed toward one long or two short objects by introducing – in the adaptation phase – a systematic backward shift of the object(s) during second saccade execution. Pre- and post-adaptation phases with no such backward shift were also tested.

2.1. Results

2.1.1. Saccade latencies

As shown in Fig. 1, on average, first saccade latency was shorter than second saccade latency (203 ms vs. 382 ms, respectively) for both one long object (1OB) and two short objects (2OB). The average latency for the first saccade was 203 ms and 202 ms for 1OB and 2OB, respectively. The average latency for the second saccade was 382 ms and 392 ms for 1OB and 2OB, respectively. The latency values are presented in Fig. 1.

**Fig. 1 – Experiment 1. Average latency (milliseconds) of the first (hatched) and second (full) saccades for one-object (1OB) and two-object (2OB) trials in the pre-adaptation, adaptation and post-adaptation phases.**

Only the 48 final trials of the adaptation and post-adaptation phases are taken into account here. Error bars are ± S.D.
F(1,3)= 28.2, p<0.015) but did not depend on phase (pre-adaptation, adaptation and post-adaptation; F<1) or object condition (one- versus two-object; F(1,3)=4.5, NS). Second saccade latency was the time separating first saccade offset from second saccade onset. The interaction between saccade (first versus second) and object condition was significant (F(1,3)= 21.3, p<0.02), corresponding to a difference between one and two objects on second saccade latency but not on first saccade latency. We suggest that this reflects an additional process in the two-object condition compared to the one-object condition which could correspond to the selection of a saccade target in the two-object condition only.

2.1.2. Saccade endpoints

Fig. 2 presents the individual time course of first and second saccade endpoints for the three phases (pre-adaptation, adaptation and post adaptation). For each subject and condition, curves correspond to the average endpoints of successive 12-point bins (see Section 5.6). Despite the variability between subjects for both first and second saccade endpoints in each object condition, subjects executed a two-saccade sequence that generally landed on each of the two objects in the two-object condition or on the beginning and end of the long X-string in the one-object condition. Such a pattern of eye movements was consistent with that expected in the procedure used here. During the pre-adaptation phase, average second saccade endpoints were similar between one- and two-object conditions. With the introduction of the intrasaccadic target back step, second saccade endpoints shifted adaptively leftward in the two-object condition, but remained relatively stable in the one-object condition. With the disappearance of the back step in the post-adaptation phase, endpoints returned progressively close to the pre-adaptation level in the two-object condition.

The amount of saccade endpoint change in the adaptation and post-adaptation phases relative to the pre-adaptation phase was calculated for each subject as follows: \( \frac{(\text{pre-adaptation endpoint} - \text{adaptation or post-adaptation endpoint})}{\text{intra-saccadic target step size}} \) (Fig. 3). Positive values correspond to a leftward saccadic endpoint shift, indicating a compensation of the backward step of the X-string(s). Globally, second saccade endpoint change depended on object condition and phase (F(1,3)=63.7, p<0.001 and F(1,3)=51.4, p<0.005). In the adaptation phase, for the one-object condition (for which the second saccade was a within-object saccade), average second saccade endpoint change was \(-0.3\pm18\%\), which did not differ significantly from 0 (Student t-test, \( t_{[3]} <1 \)). For the two-object condition, a significantly different (F(1,3)=46.6, p<0.005) pattern of results was observed for the second saccade which here was a between-object saccade. Average second saccade endpoint change was 78±9%. In the post-adaptation phase, average second saccade endpoint
change was $-8.8\pm12\%$ for the one-object condition and $16.5\pm17\%$ in the two-object condition (neither were significantly different from 0, $t_{[3]}<1$) suggesting that on average, in the post-adaptation phase, second saccade endpoints were comparable to pre-adaptation (note that the relatively large individual differences, especially for the two-object condition, indicated that extinction was not complete by the end of the post-adaptation condition for all subjects).

As can be observed in Fig. 2, despite the inter-subject variability, first saccade endpoints during the pre-adaptation phase were similar between the object conditions. During the adaptation phase, first saccade endpoints shifted leftward in the two-object condition but remained relatively stable in the one-object condition. The amount of first saccade endpoint change was calculated as above (Fig. 3) and differed significantly between object conditions (one-object, $2\pm15\%$; two-object, $27\pm14\%$; $F(1,3)=59.5$, $p<0.002$). As no intra-saccadic shift occurred during the first saccade, the first saccade endpoint change must result from the transfer of second saccade adaptation observed in the two-object condition. In the post-adaptation phase, average first saccade endpoint change did not differ between-object conditions (one-object, $-5\pm2\%$; two-object, $-6\pm7\%$; $F<1$).

2.2. Discussion

When the second saccade of a two-saccade sequence was directed toward a new object (between-object saccade), targeting errors evoked by the systematic back step of the target during the saccade were corrected for and saccade endpoints shifted adaptively in order to compensate for the error. When the second saccade was within the same object,
no such adaptation was observed. Instead, endpoints remained stable throughout the experiment despite the presence of a visual error during the adaptation phase. The targeting error introduced by the intra-saccadic target step seems not to be taken into account for the programming of within-object saccades which as a result do not compensate for the error.

When a sequence of two between-object saccades was programmed, adaptation of the second saccade, due to the systematic intra-saccadic shift of the second object, transferred to the first saccade. Such a result can be explained because the two successive saccades shared several characteristics important for transfer. Both were in the same direction and had similar amplitudes (around 3°). Additionally, adaptation is not specific to eye position (Albano, 1996).

Before further elaborating on the selectivity of adaptation to between versus within-object saccades, we had to explore an alternative explanation that could account for our results. The interesting difference between the two saccade types could also be explained by the difference of visual feedback, after the second saccade was executed, between the one- and two-object stimuli. Because of object boundaries, more visual information is available with two objects than with one object. Visual references drive adaptation (Noto and Robinson, 2001), so any difference in the amount of visual information would be crucial to adaptation and could explain why we failed to observe adaptation for within-object saccades. To avoid this possible confounding of saccade type (between vs. within saccades) and visual feedback related to object structure, we attempted to adapt within-object saccades by adaptation transfer in Experiment 2. We adapted the second saccade of a sequence directed towards two isolated targets (IT), and then tested transfer of this adaptation to our two-object conditions (one versus two-objects) and saccade position in the pre- and adaptation phases. Only the second saccade was memory-guided in these trials as stimuli were extinguished during first saccade execution (see Fig. 7B) to avoid interfering with saccadic adaptation in IT trials and therefore allowing optimal conditions for adaptation transfer. If target object selection is a prerequisite for saccadic adaptation, we hypothesize that the adaptation of a saccade that aims for a selected target will transfer to second saccades in the two-object condition but not in the one-object condition. Pre-adaptation and adaptation phases were tested in Experiment 2.

3. **Experiment 2: selective second saccade adaptation transfer**

The transfer of between-object saccade adaptation to within-object saccades was examined by adapting a second between-object saccade and testing the transfer of this adaptation to the second of a two-saccade sequence elicited in the two-object conditions (one versus two objects, corresponding to within- or between-object saccades respectively). Second saccade adaptation was obtained by having subjects make two successive saccades toward two isolated targets (IT) and by stepping the second cross back by 1° during the second saccade. The X-strings used for the object conditions were identical to those in Experiment 1 but the second saccade was memory-guided in these trials as stimuli were extinguished during first saccade execution (see Fig. 7B) to avoid interfering with saccadic adaptation in IT trials and therefore allowing optimal conditions for adaptation transfer. If target object selection is a prerequisite for saccadic adaptation, we hypothesize that the adaptation of a saccade that aims for a selected target will transfer to second saccades in the two-object condition but not in the one-object condition. Pre-adaptation and adaptation phases were tested in Experiment 2.

3.1. **Results**

3.1.1. **Saccade latencies**

As seen in Fig. 4, the average first saccade latency was shorter than second saccade latency (152 ms vs. 342 ms, \(F(1,3)=144.21, p<0.0001\)), as expected because first saccades were reactive and second saccades were volitional (either visually guided in IT trials or memory-guided in object trials). First saccade latencies were reactive and therefore shorter than those observed in Experiment 1 (volitional saccades). As in Experiment 1, second saccade latencies differed according to the second saccade type. Latencies did not differ between the pre- and adaptation phases (\(F<1\)) and there was no interaction with saccade position (\(F<1\)). There was a global effect of stimulus condition on latency (\(F(2,6)=14.93, p<0.005\)): two-object and IT latencies did not differ significantly but both showed longer latencies than one-object trials. This effect depended on the saccade position in the sequence: first saccade latencies in one-object trials (144 ms), two-object trials (147 ms), and IT trials (164 ms) did not differ (\(F(1,3)=1.91, NS\)) whereas second saccade latencies in one-object trials (305 ms) were shorter than those observed in both two-object and IT trials (351 ms, \(F(1,3)=27.42, p<0.01; 371 ms, F(1,3)=5.29, p<0.05\) respectively). Importantly for our purpose, the interaction between-object conditions (one-object vs. two-objects) and saccade position (1st vs. 2nd) was significant (\(F(1,3)=75.23, p<0.001\)).
3.1.2. Saccade endpoints

Fig. 5 presents individual time courses of first and second saccade endpoints (lower and upper curves) for the three stimulus conditions, before and during saccadic adaptation evoked by the backward step of the second target in IT trials. For each subject, each phase and each stimulus condition, average first and second saccade endpoints were calculated for bins of successive trials (see Section 5.6). In the pre-adaptation phase, second saccade endpoints were similar between the one- and two-object conditions. In IT trials, the intra-saccadic second target back step evoked an adaptive leftward shift of second saccade endpoints that can be seen clearly for all four subjects. During the course of second saccade adaptation, the endpoints of the first of the two saccades shifted slightly leftward as well. However, second saccade endpoints shifted leftward during the adaptation phase only in the two-object condition and remained relatively stable throughout the two phases in the one-object condition. Thus, only endpoints of second saccades that aimed for a new object shifted concurrently with second saccade adaptation in IT trials.

The saccadic endpoint changes relative to the pre-adaptation phase [(pre-adaptation endpoint – adaptation endpoint)/intra-saccadic target step size] are presented in Fig. 6A. Individual averages for each stimulus conditions are given in Figs. 6B–D. In the IT condition, positive relative saccade endpoint change indicates that the leftward shift of saccade endpoints compensated for the intra-saccadic target step. As such trials were interspersed with object trials, an endpoint change of the second saccade directed toward a second spatially extended object (between-object saccades in two-object trials) or that explored the same object (within-object saccades in one-object trials) will be interpreted as a modification obtained by adaptation transfer.

Globally, relative endpoint change depended on stimulus condition (F(2,6)=266.2, p<0.0001). A similar pattern was found in IT and two-object conditions (F(1,3)=2.9, NS) while both differed from the one-object condition (F(1,3)=1063.9 and F(1,3)=192.7, ps<0.0001, respectively). As expected, stimulus condition interacted with the position of the saccade in the sequence (F(2,6)=12.9, p<0.01). No interaction with saccade position was found when analyses of variance were restrained to IT and two-object conditions (F<1) but interactions were found when the one-object condition was contrasted to IT or to two-object conditions (F(1,3)=14.3 and F(1,3)=18.1, ps<0.05, respectively). These interactions reveal that the average second saccade endpoint change in the two-object condition (57±7%) was not significantly different from the 62±4% change observed in the IT condition (F(1,3)=6.52, p<0.09). Both values were different from 0% (Student t-tests, t[3]=29.23 and t[3]=17.59, ps<0.001) but also from 100% (Student t-tests, t[3]=17.91 and t[3]=13.27, ps<0.001). The second saccade

![Fig. 5](image-url)

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**Fig. 5** – Experiment 2. Individual saccade endpoints of the first (lower curves) and second (upper curves) saccades for IT, one- and two-object trials, for the two successive phases. The vertical gray arrow indicates the start of the adaptation phase (2nd IT backward step from trial 55). Horizontal gray bars represent positions of IT1, IT2 and IT2′, respectively.
endpoint change in the one-object condition (4±9%) was not significantly different from 0% (Student t-test, t[3]=0.75, NS) but was significantly different from that observed in both IT and two-object conditions (F(1,3)=106.1, p<0.0001 and F(1,3)=96.2, p<0.0001, respectively).

The amount of second saccade adaptation transfer from IT to two-object trials can be calculated as the ratio of second saccade endpoint change of the latter to second saccade endpoint change of the former. As can be inferred from Fig. 6A, this ratio was 92±7% (difference from 100% transfer did not reach significance, Student t-test, t[3]=2.51, NS), suggesting that second saccade adaptation induced by the intra-saccadic target step in IT trials transferred completely to the second saccade in the two-object condition.

It should be noted that a small change of first saccade endpoints was observed for both the IT (21±8%) and two-object (20±9%) conditions. Both were significantly different from 0% (Student t-test, t[3]=4.96 and t[3]=4.28, ps<0.05) and did not differ from each other (F<1). The small change observed in the one-object condition (~2±8%) was not significantly different from 0% (Student t-test, t[3]=0.50, NS) and differed from both IT and two-object conditions (F(1,3)=31.5, p<0.01 and F(1,3)=38.7, p<0.01 respectively). A concurrent modification of the first saccade with 2nd saccade adaptation was already found in Experiment 1, but both saccades were volitional. Here, the first saccade was reactive while the second was volitional but we still observed a first saccade modification. Such a result could be explained in terms of partial transfer of volitional saccade adaptation to reactive saccades (Collins and Doré-Mazars, 2006; Alahyane et al., 2007). However, if this explanation is correct, visual feedback about the first IT probably prevented a stronger transfer. Intriguingly, first saccades followed by a within-object saccade (one-object condition) did not show any change during the adaptation phase. We would have expected the first saccade change to concern all the first saccades as IT, one-object, and two-object trials were mixed and as all first saccades were between-object. They differed only in that they were followed by a within- or between-object saccade. This surprising result may suggest that the specific type of saccade sequence plays a role in the transfer of adaptation.

3.2. Discussion

In a sequence of two between-object saccades, we adapted the second saccade and tested transfer of adaptation to two other saccades of comparable amplitude. Adaptation transferred to another between-object saccade but did not transfer to within-object saccades.

Previous studies have suggested that between-object saccades are coded on the basis of target selection, while within-object saccades do not depend on target selection but are coded as fixed motor vectors. In light of these previous studies, we propose that the absence of transfer of adaptation from between-object saccades to within-object saccades does indeed reveal different coding. Furthermore, the results...
suggest that target selection is a crucial determinant of saccadic adaptation transfer.

4. General discussion

Adaptation was evoked directly or indirectly (by transfer) and was successful only when an object was selected as saccade target. In Experiment 1, the systematic shift of the whole configuration during the second saccade execution led to the adaptation of the second saccade, but only when a new object was selected as the saccade target. When the saccade was directed within the same object, no adaptation occurred. These results suggest that target selection plays a primary role in saccadic adaptation. Because of differences in visual feedback relative to object structure between the two conditions (see discussion of Experiment 1), Experiment 2 was carried out, in which the second saccade of a two-saccade sequence toward two isolated targets (IT) was adapted by introducing a systematic backward step of the second target. We examined whether this adaptation transferred to the second of a two-saccade sequence that explored one long or two short X-strings. We found a clear second saccade endpoint change in two-object trials, suggesting a second saccade adaptation transfer from IT trials to two-object trials. Such a result was expected because despite the difference of stimulus size (two IT vs. two spatially extended objects), both second saccades shared characteristics important for transfer, and among them is the fact that both aimed for a specific location in visual space. In spite of the adaptive change observed in IT trials, and in the two-object condition due to adaptation transfer, interleaved trials in which the second saccade explored the same object did not show any second saccade modifications. Such a result suggests that target selection could prevail over the vector metrics in determining adaptation transfer. Taken together, the present study suggests that target selection is not only crucial for the adaptive process itself, but is also determinant for saccadic adaptation transfer.

When target selection is the primary determinant of the saccade vector, as would be the case for between-object saccades, targeting errors such as those mimicked by the intra-saccadic target step paradigm would be important to correct so that future saccades are precise. Indeed, in both experiments of the present study, an intra-saccadic change of target position led to the adaptive modification of such saccades. Furthermore, saccadic adaptation obtained with discrete targets transferred to between-object saccades that aimed for a spatially extended object, confirming the idea that the saccadic system computes the center of gravity of such stimuli and specifically aims for it (Kowler and Blaser, 1995). This is also in agreement with the notion that a distinct, localized target for the saccade is necessary for adaptation to take place (Noto and Robinson, 2005).

Previous studies (cited in the Introduction section) suggest that, when the second saccade explores the same object, the saccade vector depends on object size rather than on a particular position in the object. Therefore, within-object saccades would be coded as a motor vector of fixed magnitude and would not be influenced by the position of the first saccade that led the eyes into the object. According to this assumption, there is no target selection as the endpoint of the within-object saccade corresponds to the addition of the motor vector to the first saccade endpoint. Therefore, even if spatial information about object location was modified after the second saccade execution, it would not influence the motor vector of the within-object saccade. The absence of adaptation of within-object saccades (Experiment 1) supports this claim by showing that visual feedback about the endpoint of the saccade is not taken into account to adapt future behavior. The absence of between-object saccade adaptation transfer to within-object saccades (Experiment 2) further reinforces the idea that the vector does not aim for a specific target location as between-object saccades do, but would execute a preplanned motor vector dependent on object size. Indeed, Vergilino and Beauvillain (2000) showed that the amplitude of within-object saccades was modified when the length of a letter string was modified, but with a time cost.

In conclusion, our findings that within-object saccades do not adapt (directly or indirectly) suggest that the selection of a visual target object appears necessary for saccadic adaptation to take place. Because the delays necessary for sensory–motor processing are longer than the duration of the saccade, the control of saccade accuracy relies on post-saccadic visual feedback and systematic errors lead to a recalibration of the transformation of visual target information into a motor command so as to eliminate them. Our conclusion could appear trivial when saccadic adaptation is investigated with poor visual displays that elicit only targeting (between-object) saccades but not when it is studied with more complex visual displays such as reading or natural scenes in which both targeting and exploratory (within-object) saccades are made. The intra-saccadic target shift mimics saccadic under- or overshoot caused by oculomotor deficits, such as lesions of extra-ocular muscles. In a classical laboratory test, these patients typically show targeting errors that disappear after several days (Abel et al., 1978). If exploratory saccades do not adapt, in natural situations these patients would still present deficits that would not be captured by standard clinical tests. It thus appears of clinical relevance to identify how different saccades might respond differently to systematic oculomotor errors.

5. Experimental procedures

5.1. Subjects

In each experiment, four trained subjects with normal vision participated. Two of them were authors and two others were experienced in various experiments related to eye movement study but naive relative to the goal of the experiment. The two naive subjects were not the same across the two experiments.

5.2. Instruments and eye movement recording

The experimental sessions took place in a dimly lit room. Subjects were seated 70 cm away from the screen and their head kept stable with a submaxillar dental print and forehead rest. 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 arc min and a linear output over 12° of visual angle. Viewing was binocular but only the movements of the right eye were monitored. Signal from the oculometers was sampled every 2 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 controls the scope allowed a change of display in 1 ms. Complete details of the eye movement recording apparatus, calibration procedure and numerical data processing can be found elsewhere (Beauvillain and Beauvillain, 1995).

Each session began with a calibration procedure in which the subjects were required to sequentially fixate five positions along a horizontal 12°-long axis. In order to check the accuracy of the eye movement recording with respect to the previous calibration procedure, each experimental trial was preceded and followed by a calibration bar displayed 6° to the left and right of the screen’s center. If the difference between this position and that measured previously during the complete calibration was above a given threshold (±15 arc min), a new complete calibration was automatically renewed. If the computer detected an accurate fixation on the left calibration bar, this bar was replaced by the fixation target (T₀), indicating the beginning of the next experimental trial.

5.3. Stimuli

The visual stimuli were 0.5°x1° green X’s on a black background, and their apparent luminance was set at 0.40 cd/m² with a Minolta LS-110 luminance meter. The stimuli used in one- and two-object conditions were identical in Experiments 1 and 2. Two degrees to the right of the fixation cross (T₀), a 6° wide peripheral string of X’s was presented, twelve X’s or six and five X’s separated by a blank for the one-object and two-object conditions respectively (Fig. 7B). Saccades directed toward spatially extended targets (or to a group of discrete elements) generally land on a central position within the visual configuration, called the “center of gravity” (Coren and Hoenig, 1972). The center of gravity calculation would be the “default” option of the saccade targeting system (Findlay and Walker, 1999). Accordingly, a great majority of fixations were near of the center of objects in natural scenes (Melcher and Kowler, 2001). Therefore, we expected that saccades would be directed toward the center of gravity of each X-string in the two-object condition. However, the more the peripheral object’s size increases, the higher the probability that a saccade lands on a position close to its beginning and that a second within-object saccade is executed. Such a behavioral pattern is well known in reading research (e.g. McConkie et al., 1989). Therefore we expected that, in most cases, the long string of X’s used in the one object condition would be explored by a sequence of two saccades.

Fig. 7 – Stimuli and experimental design. Stimuli were 0.5° wide crosses. (A) IT condition (Experiment 2): two isolated targets (T₁ and T₂) were used corresponding to the fourth and tenth X of the long string of Xs. (B) Object conditions. Objects were either one long string of 12 Xs (one-object condition) or two short strings of 6 and 5 Xs separated by one space (two-object condition). (C) Sequence and timing of stimulus presentation when a two-saccade sequence was executed in IT trials. T₁ and T₂ were displayed simultaneously to T₀ offset. During the saccade made to T₂, T₁ was extinguished and T₂ stepped backward to T₂' in the adaptation phase but remained at the same position as T₂ in pre-adaptation phase (not shown here). Thick lines represent visual stimuli and dashed lines represent eye position. T₀: fixation cross; T₁ and T₂: first and second isolated targets; SL: first saccade latency. (D) Sequence and timing of stimulus presentation when a two-saccade sequence was executed in object trials (Experiment 2). The objects were displayed simultaneously with T₀ offset and disappeared during the first saccade execution. No visual stimuli were available for the subsequent saccade. Other conventions as in (C).
In Experiment 2, stimuli used in isolated target trials (IT) consisted of two X’s displayed at 4° and 7° eccentricity (T₁ and T₂) to the right of fixation target (T₀) (see Fig. 7A). Note that locations of isolated targets used in IT condition were selected to correspond to probable endpoints of the first and second saccades in object conditions.

5.4. Procedure

In Experiment 1, a trial began when the foveal fixation target and peripheral X-string(s) appeared. 300 ms later, the offset of the foveal fixation target (T₀) signaled the subjects scan the object(s). Subjects were required to explore the objects without any particular instruction about the number of saccades to be made. During adaptation trials, the entire peripheral stimulus was shifted 1° to the left during the second saccade and remained so until the end of the trial. The shift was done when the eye crossed an invisible boundary placed at the center of the sixth X. During the pre-adaptation and post-adaptation phases, no such shift occurred and the stimulus remained at the same eccentricity throughout the entire trial. Finally, the object(s) disappeared when the eyes crossed an invisible boundary placed 1° to their right.

In Experiment 2, during isolated target (IT) trials, after the eyes remained on the fixation point (T₀) for 300 ms, two peripheral X’s (T₁ and T₂) were displayed simultaneously with the offset of T₀. Subjects were instructed to make a saccade first to T₁ and then to T₂. In order to adapt the second saccade, the first target disappeared and the second target was stepped 1° to the left (to T₂) during the saccade to the second target (Fig. 7C). This was done when the eye crossed an invisible boundary placed at the center of the sixth X. During the pre-adaptation phase, no intra-saccadic target step occurred and T₂ remained at the same eccentricity throughout the entire trial. The extinction of the first target during second saccade execution prevented subjects from comparing the position of the second target to the position of the first target previously fixated. Indeed, in pretests where both the first and second target stepped backward during the second saccade, subjects always noticed the step, in particular of the first target. In adaptation trials where the first target disappeared during the saccade that aimed for the second target, none of the participants noticed the backward step of the second IT.

Object trials were interleaved with IT trials, but there was never a step of the objects. Instead, objects disappeared during first saccade execution (when the eyes crossed an invisible boundary placed at 1° to the right of the fixation point) (Fig. 7D). Thus, the second saccade was memory-guided while the first saccade was visually guided. Subjects were instructed to scan these stimuli as if they were always available. Object extinction during the first of the two saccades was necessary for two reasons. First, to make sure that visual feedback before and after second saccade execution between one- and two-object conditions was the same and second, to avoid interference with second saccade adaptation in IT trials. This allowed us to examine the transfer of the IT second saccade adaptation to second saccades executed in the object conditions in an optimal manner.

5.5. Design

In Experiment 1, each experimental block consisted of 48 pre-adaptation trials followed by 96 adaptation trials in which the X-string(s) shifted backward during the second saccade, and then 72 post-adaptation trials with no shift. One experimental block therefore consisted in 216 trials. Each subject took four blocks on different days, two for each object condition, and the order was counterbalanced across subjects.

In Experiment 2, each experimental session included two phases. In the pre-adaptation phase (consisting of 54 trials), one- and two-object trials were interspersed with equal probability within isolated targets trials (i.e. 18 trials, 33% for each condition). The adaptation phase consisted of 192 trials in which one- and two-object trials were interspersed at low probability (24 trials or 12.5% each) within the adaptation IT trials (144 trials or 75%). During the adaptation phase, for each set of eight successive trials, there were six IT trials and one trial of each object condition. Thus, there was at least one IT trial between two successive object trials, in order to maintain the adapted state of the second saccade. A session (total of 246 trials) was repeated six times by subjects on different days. After completion of the six sessions, the number of trials per subject was of 108 trials each in the IT, one- and two-object conditions in the pre-adaptation phase, 864 trials in the IT condition and 144 trials in each object condition in the adaptation phase.

5.6. Data analysis

In Experiment 1, 4% of the trials were excluded from the analyses because of a lack of accuracy in the eye position measurement (2%), blinks (1%), or trials in which saccade latency was shorter than 50 ms (1%). In addition, trials in which a single or three or more saccades occurred (single saccades: 9% and 3%; three or more saccades: 4% and 1% for one- and two-object conditions respectively) and trials in which the second endpoint was before the invisible boundary used for the intra-saccadic target step were discarded (1% for both one- and two-object conditions). After elimination, the average number of observations per subject was 74±5 (one-object), 92±2 (two-object) in the pre-adaptation phase, 172±5 (one-object), 176±4 (two-object) in the adaptation phase and 114±6 (one-object), 138±3 (two-object) in the post-adaptation phase.

In Experiment 2, 13% of trials were excluded from the analyses for the following reasons: lack of accuracy in the eye position measurement (5%), blinks (2%), or first saccade latencies shorter than 50 ms (6%). In addition, trials in which sequences of single or three or more saccades occurred were not taken into account (single saccades: 2%, 5% and 3%; three or more saccades: 6%, 6% and 5% for IT, one- and two-object conditions respectively). After these eliminations, the average number of observations per subject was 85±14 (IT), 70±21 (one-object), 73±17 (two-object) in the pre-adaptation phase and 671±100 (IT), 89±18 (one-object), 96±12 (two-object) in the adaptation phase.

For the time course analyses, in Experiment 1, the pre-adaptation phase (trial ranks 1 to 48) was divided into 4 bins of 12 ranks, the adaptation phase (trial ranks 49–144) into 8 bins.
of 12 ranks, and the post-adaptation phase (trial ranks 145–216) into 6 bins of 12 ranks. Over the four sessions of Experiment 1, each trial rank was tested twice per subject, per object condition, and per phase. In Experiment 2, the pre-adaptation phase (trial ranks 1 to 54) was divided into 6 bins of 9 ranks, for each stimulus condition. Over the six sessions of Experiment 2, each trial rank was tested twice per subject and per stimulus condition in the pre-adaptation phase. The adaptation phase (trial 55 to 246) was divided into 12 bins of 16 ranks (see the Design section). Over the six sessions, each rank was tested 4–5 times (IT) and once for 12 of the 16 ranks (object conditions).

The average adapted endpoint was calculated on all pre-adaptation trials, the final half of the adaptation trials (so as to compare an equal number of trials for each phase and to limit analyses to trials which clearly differentiated the adaptation phase in terms of saccade endpoints) and the last 48 trials of the post-adaptation phase in Experiment 1. For the analyses of variance on latency (ANOVA), a 2×2×3 factorial design was adopted in Experiment 1. Factors were object condition (one vs. two), saccade (first vs. second saccade of the sequence) and phase (pre-adaptation, adaptation, post-adaptation). For the ANOVA on % endpoint change, the same factors were used but the phase had only two modalities (adaptation and post-adaptation). In Experiment 2, a 3×2×2 design was adopted (stimulus condition: IT, one-object, two-object; saccade: first vs. second; phase: pre- vs. adaptation) for latency, and a 3×2 design was used for endpoint change (stimulus condition; saccade). When indicated, Student t-tests were also performed.

REFERENCES