Saccadic adaptation maintains saccade accuracy and has been studied with targeting saccades, i.e. saccades that bring the gaze to a target, with the classical intra-saccadic step procedure in which the target systematically jumps to a new position during saccade execution. Post-saccadic visual feedback about the error between target position and the saccade landing position is crucial to establish and maintain adaptation. However, recent research focusing on two-saccade sequences has shown that exploring saccades, i.e. saccades that explore an object, resists this classical intra-saccadic step procedure but can be adapted by systematically changing the main parameter used for their coding: stimulus size. Here, we adapted an exploring saccade and a targeting saccade in two separate experiments, using the appropriate adaptation procedure, and we tested whether the adaptation induced on one saccade type transferred to the other. We showed that whereas classical targeting saccade adaptation does not transfer to exploring saccades, the reciprocal transfer (i.e., from exploring to targeting saccades) occurred when targeting saccades aimed for a spatially extended stimulus, but not when they aimed for an isolated target. These results show that, in addition to position errors, size errors can drive adaptation, and confirm that exploring vs. targeting a stimulus leads to two different motor planning modes.

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Keywords: Saccade, Adaptation, Size, Exploring saccade, Targeting saccade, Within-object saccade, Between-object saccade
saccades fall short of the target (or overshoot, depending on the paresis), and adaptation reestablishes correct targeting (Abel et al. 1978). In the laboratory, adaptation is simulated by stepping the target during saccade execution, causing an artificial targeting error (McLaughlin 1967; Deubel et al. 1986). With this classic intra-saccadic step procedure, saccade amplitude progressively becomes appropriate to the post-saccadic target. It has been shown that mechanisms that compare pre- and post-saccadic visual information (real or predicted) of the target could be the guiding signal for adaptation (Bahcall and Kowler 2000; Noto and Robinson 2001; Collins et al. 2009).

This oculomotor plasticity is specific to the adapted saccade motor vector (e.g. Watanabe et al. 2000; Collins et al. 2007a), but also to saccade type. For instance, adaptations of reactive saccades executed in response to a sudden stimulus vs. volitional saccades toward a stable stimulus are partly independent: despite a similar motor vector, the adaptation of volitional saccades transfers to reactive saccades but not the reverse (Deubel 1995; Fujita et al. 2002; Collins and Doré-Mazars 2006; Alahyane et al. 2007; Hopp and Fuchs 2010).

Recent studies on two-saccade sequences have investigated another dissociation between saccade types, according to the action goal: saccades targeting a new object for the first time (also called “between-object saccades”) versus those exploring a currently fixated object (also called “within-object saccades”). Indeed, a growing set of behavioral data shows that exploring saccades are coded on the basis of object size, whereas targeting saccades are coded on the basis of object position (e.g. Vergilino and Beauvillain 2001; Vergilino-Perez and Findlay 2006; Doré-Mazars et al. 2006). Indeed, using a two-saccade sequence in which the second saccade either aimed for or explored an object, it was previously shown that exploring saccade amplitude increased with object size (e.g. Beauvillain et al. 2005; Vergilino and Beauvillain 2000), suggesting that size is the parameter used to plan this particular saccade type. It was also shown that while exploring saccade amplitude did not compensate for the initial landing position variability, targeting saccade amplitude did (Beauvillain et al. 2005; Doré-Mazars et al. 2006). Two recent studies on saccadic adaptation have confirmed this differential coding between exploring vs. targeting saccades. The first showed that exploring saccades resist the classic intra-saccadic step procedure and that targeting saccade adaptation does not transfer to exploring saccades. These results supported the idea that stimulus position is not taken into account in the planning of exploring saccades (Collins et al. 2007b). The second study (Lavergne et al. 2010) used a systematic modification of stimulus size (lengthening or shortening) during the execution of the exploring saccade, and this did lead to saccadic adaptation. Taken together, the results of these two studies favor dissociation between targeting and exploring saccades which can be revealed by their differential susceptibility to adaptation.

The aim of the current study is to complement the previous results by examining whether the adaptation of exploring saccades, using the intra-saccadic size-change procedure (Lavergne et al. 2010), transfers to targeting saccades (Experiment 1). In Experiment 2, we replicated the finding that the adaptation of targeting saccades transfers to exploring saccades (Collins et al. 2007b). We expected adaptation of exploring saccades to occur with the intra-saccadic size-change procedure, and adaptation of targeting saccades to occur with the intra-saccadic step procedure. The central question was whether such adaptations are selective, i.e., whether they transfer from one saccade type to the other.

2. Results

Both experiments consisted of three successive phases: pre-adaptation, adaptation and post-adaptation phases. A change in the characteristic of the stimulation was induced during the execution of the second saccade in the adaptation phase only. In this phase, only one stimulus was shown: a single-12X-object (Experiment 1) or two-object (Experiment 2). In pre- and post-adaptation phases, different stimuli were presented (isolated-target-pair, single-12X-object, single-10X-object, two-object: see Fig. 1 and Section 4.2) and extinguished during the first saccade execution in order to avoid visual feedback, thus no intra-saccadic change occurred during the second saccade. To test the retention of adaptation in the same stimulus condition and the transfer of adaptation to other saccade types and conditions, pre- and post-adaptation values were compared.

2.1. Saccade latencies

Phase did not affect first or second saccade latencies in any stimulus condition (all Fs and Student t-tests non-significant) except for Experiment 1 in which first saccade latencies were shorter in the post-adaptation phase than in the pre-adaptation phase both for the isolated-target-pair condition (183±8 ms and 202±14 ms respectively, \( t(5)=6.16, p<.002 \)) and the two-object condition (181±11 ms and 189±9 ms respectively, \( t(5)=3.13, p<.03 \)). This decrease is probably due to training. Overall, mean latencies were shorter for first saccades than for second saccades, in both Experiments 1 (186±10 ms and 232±29 ms respectively) and 2 (190±15 ms and 215±30 ms). This was expected since the first saccade was reactive and visually-guided while the second was memory-guided.1

2.2. Experiment 1: Saccadic adaptation induced by a size change

In Experiment 1, an exploring saccade was adapted by systematically shortening the size of the single-12X-object.

2.2.1. Saccadic adaptation in the single-12X-object condition

First saccade amplitude was 3.9±0.4° and remained stable across Phases (\( F(1,5)=1.2, \) ns), see Table 1.

As expected, second saccade amplitude was affected by Phase (\( F(2,10)=6.9, p<.02 \)): there was a progressive and significant decrease from pre-adaptation to adaptation (see Fig. 2b; \( F(1,5)=13.8, p<.02 \)). Adaptation was retained in the

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1 The term “memory-guided” refers to the fact that second saccades were not visually guided as the stimulus was extinguished during the execution of the first saccade. “Memory-guided” thus designates a methodological procedure here rather than any reference to visual or motor representation stored in memory.
post-adaptation phase: amplitude in this phase did not differ from that in the adaptation phase ($F(1,5)=0.1$, ns.).

A way to measure the adaptation evoked by the size change is the amount of compensation: \(\left(\frac{\text{pre-adaptation amplitude} - \text{post-adaptation amplitude}}{\text{size change}}\right)\times 100\). Here, size change equals 1°. This calculation allows a comparison of amplitude changes relative to the size change. Zero compensation corresponds to the case when no amplitude change occurred, i.e. the size change had no effect. Total (100%) compensation indicates that the amplitude change fully compensated for the stimulus size change. Here, compensation was 69±28% (see Fig. 3), and which was significantly

<table>
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<th>Table 1 – Experiment 1: Mean amplitudes of first and second saccades per condition. Values in italics correspond to standard deviations.</th>
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<tr>
<td>Experiment (deg)</td>
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<tr>
<td>First saccade</td>
</tr>
<tr>
<td>Second saccade</td>
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Fig. 1 – Physical (a) and temporal (b, c, d) characteristics of stimuli in Experiments 1 and 2. a Fixation cross, and to the right the 5 possible stimuli used during the experiment: the 4 upper stimuli elicited a 2-saccade-sequence and the one at the bottom elicited a single saccade. b, c Time course of a trial in pre- and post-adaptation phases, for stimuli eliciting a 2-saccade sequence (b) or a single saccade (c): at fixation cross (FC) offset, a stimulus was displayed until a saccade was initiated, and was extinguished thereafter. In the pre-adaptation phase, the stimulus was one of the 5 possibilities illustrated in a. In the post-adaptation phase, the stimulus was randomly chosen among 4 possible stimuli: the single-10X-object was not shown. d Time course of a trial in the adaptation phase in Experiment 1: at fixation cross offset, the single-12X-object was displayed and replaced by the single-10X-object during second saccade execution. In Experiment 2, the two-object stimulus was initially displayed 2.3° right from fixation cross and stepped back from 1° at second saccade onset.
greater than 0% (t(5)=4.1, p<.005) and was not smaller than 100% (t(5)=1.2, ns), indicating that adaptation occurred and compensated for the size change.

Another way to assess the amplitude change is to compare it to that of the single-10X-object condition in the pre-adaptation phase. Indeed, in the adaptation phase a 12X string was shortened to a 10X string. We can therefore examine whether the adapted saccade is comparable to non-adapted saccades exploring a 10X object. Compared to pre-adaptation amplitudes in the single-10X-object condition, in the pre-adaptation phase, amplitudes in the single-12X-object condition were, as expected, larger (t(5)=6.4, p=.0005, see Table 1). However, this difference disappeared in both adaptation (t(5)=0.9, ns.) and post-adaptation phases (t(5)=1.1, ns.).

The intra-saccadic size change used in this experiment led to a progressive amplitude reduction. By the end of the adaptation phase, the amplitude change compensated for the size change and was comparable to non-adapted saccades executed within objects that were 1° smaller. This adaptive state was maintained in absence of visual feedback in the post-adaptation phase. The next sections ask whether the adaptation of the exploring saccade executed within a single object transferred to targeting saccades executed between isolated targets or spatially extended objects.

2.2.2. Transfer of adaptation in the isolated-target-pair condition

First and second saccade amplitude remained stable at 4.7±0.5° and 3.6±0.9° (mean values averaged over phases) respectively between pre-and post-adaptation phases (t(5)=1.5, ns. and t(5)=1.7, ns. respectively), indicating that exploring saccade adaptation did not transfer to targeting saccades executed between two isolated targets.

As in the previous section, the compensation rate was computed on second saccade amplitude (27±38%, see Fig. 3), and was significantly smaller than 100% (t(5)=4.7 p<.003) but not greater than 0% (t(5)=1.8, ns) indicating that the second saccade did not compensate for the size change. This confirms that the adaptation of the exploring saccade did not transfer to the second targeting saccade in the isolated-target-pair condition.
condition, as rates were lower in this condition (t(5)=3.9, p<.01).

2.2.3. Transfer of adaptation in the two-object condition
First saccade amplitude was 4.0±0.3° and did not differ between pre- and post-adaptation (t(5)=0.8, ns). Second saccade amplitude, however, decreased from 4.0±0.5° to 3.5±0.5° (t(5)=5.2, p<.003), suggesting that the exploring saccade adaptation transferred to the second of two targeting saccades.

Compensation rate was 57±27% and did not differ from that in single-12X-objects (t(5)=1.2, ns; see Fig. 3). However, comparisons to 0% (t(5)=5.2, p<.002) and 100% (t(5)=3.9, p<.01) indicated that the amplitude modification was present but did not fully compensate for the size change as the amount differed from both values. This result suggests a partial transfer of exploring saccade adaptation to targeting saccades that aimed for a spatially extended object. Compared to that of the isolated-pair condition, compensation rate was significantly greater (see Fig. 3, t(5)=2.1, p<.04) in the two-object condition, confirming that transfer of adaptation was more important for the two-object compared to the isolated-target-pair condition.

This result suggests a partial transfer of exploring saccade adaptation to targeting saccades that aimed for a spatially extended object.

In summary, we successfully adapted an exploring saccade by using an intra-saccadic size change procedure. This adaptation did not transfer to targeting saccades unless the targets were spatially extended objects.

2.3. Experiment 2: Saccadic adaptation induced by a position step
The same design as in Experiment 1 was used, only the adaptation procedure differed: the two-object stimulus stepped 1° backward. In order to keep the same design as in Experiment 1, single-10X-object stimuli were also presented in the pre-adaptation phase. However, they could not be used to compare amplitude reduction in the adaptation phase, and the data were therefore not analyzed.

2.3.1. Saccadic adaptation in the two-object condition
Phase did not affect first saccade amplitude (F(2,6)=0.7, ns.) which was 3.8±0.3° and remained stable throughout the three phases (see Table 2).

As expected, second saccade amplitude was affected by Phase (F(2,6)=14.6, p<.006), due to a progressive and significant decrease from pre-adaptation (4.1±0.4°) to adaptation (3.5±0.3°) phases (F(1,3)=34.7, p<.009) indicating that adaptation occurred (see time course in Fig. 4). Adaptation was maintained in the post-adaptation phase, as the average amplitude (3.5±0.5°) still differed from pre-adaptation (F(1,3)=16.6, p<.03) but not from adaptation (F(1,3)=1.7, ns).

As in Experiment 1, compensation rates were computed on second saccade amplitudes. Here, we related the amplitude change to the step size (rather than size change), which corresponds to 1°. Compensation was 61±29% (see Fig. 5) which was greater than 0% (t(3)=4.2, p<.01) and not smaller than 100% (t(3)=2.1, ns.), indicating that adaptation occurred and compensated for the step.

2.3.2. Transfer of adaptation in the isolated-target-pair condition
First saccade amplitude was 4.5±0.2° and did not vary from pre- to post- adaptation phases (t(3)=0.5, ns.), however, second saccade amplitude significantly decreased from 3.4±0.5° to 2.8±0.7° (t(3)=4.2, p<.02), indicating that second-saccade adaptation transferred to the second saccade in the isolated-target-pair condition. Compensation rate in the isolated-pair-condition was 57±28% (see Fig. 5), which was not different from compensation in the two-object condition (t(3)=1.0, ns) but was greater than 0% (t(3)=4.0, p<.01) and smaller than 100% (t(3)=3.0, p<.03), indicating that adaptation transferred to the second saccade but did not completely compensate for the step.

2.3.3. Transfer of adaptation in the single-12X-object condition
First saccade amplitude was 3.7±0.3° and remained stable from pre- to post-adaptation phase (t(3)=0.3, ns.).

Second saccade amplitude was 4.0±0.4° and did not change between Phases (t(3)=2.1, ns) as confirmed by analyses on compensation rate (14±32%, see Fig. 5) which did not differ from 0% (t(3)=0.9, ns.), but was smaller than both 100% (t(3)=5.4, p<.01) and than the two-object compensation rate (t(3)=3.5, p<.02). Compared to that of the isolated-pair condition (57±28%), this compensation rate was significantly lower (see Fig. 5, t(3)=3.0, p<.03) in the single-12X-object condition, confirming that transfer of adaptation was more important in the isolated-pair compared to the single-12X-object condition.

Table 2 - Experiment 2: Mean amplitudes of first and second saccades per condition. Values in italics correspond to standard deviations.

<table>
<thead>
<tr>
<th>Experiment 2</th>
<th>Pre-adaptation phase</th>
<th>Adaptation phase (position step)</th>
<th>Post-adaptation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude (deg)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First saccade</td>
<td>4.5</td>
<td>3.7</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>(0.2)</td>
<td>(0.3)</td>
<td>(0.4)</td>
</tr>
<tr>
<td>Second saccade</td>
<td>3.4</td>
<td>4.1</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td>(0.5)</td>
<td>(0.4)</td>
<td>(0.4)</td>
</tr>
</tbody>
</table>
Overall, the systematic backward step of the two-object stimulus during the second saccade execution induced saccadic adaptation of this saccade, which transferred to the second targeting saccade in the isolated-target-pair condition, but not to the second saccade exploring the single-12X-object stimulus.

3. General discussion

In this study, we adapted exploring and targeting saccades in two separate experiments using specific procedures: the intra-saccadic target step for targeting saccades (e.g. McLaughlin 1967) and the intra-saccadic size-change for exploring saccades (Lavergne et al. 2010). Targeting saccade adaptation did not transfer to exploring saccades of similar amplitude. Exploring saccade adaptation transferred partially to targeting saccades when they aimed for a spatially-extended object, but not when they aimed for an isolated target.

3.1. The error signal driving exploring saccade adaptation

In Experiment 1, we successfully adapted an exploring saccade by systematically shortening the explored stimulus, as in a previous study (Lavergne et al. 2010). Here we showed that this adaptation was maintained in the absence of visual feedback in the post-adaptation phase. Studies using the classical intra-saccadic step of the target showed that the visual error between the target position and the saccade endpoint drives adaptation (see Péléisson et al. 2010 for a review). In the case of exploring saccade adaptation, no such information about target position is used. Indeed, exploring saccades do not aim for a particular position but are coded as a fixed vector to be applied irrespective of the initial position of the eyes in the object (Beauvillain, et al. 2005). Moreover, it has been shown that a position step did not induce adaptation of exploring saccades (Collins et al. 2007b Experiment 1), probably because the intra-saccadic step procedure leads to saccadic adaptation only if a target is selected (Madelain et al. 2010), which is not the case for exploring saccades. Thus, position seems rejected as a signal driving exploring saccade adaptation.

Overall, the systematic backward step of the two-object stimulus during the second saccade execution induced saccadic adaptation of this saccade, which transferred to the second targeting saccade in the isolated-target-pair condition, but not to the second saccade exploring the single-12X-object stimulus.

Fig. 4 – Experiment 2: Time course of first (a) and second (b) saccade amplitude averaged across subjects, as a function of trial rank per stimulus type and phase. One point corresponds to amplitude averaged across 3 trials. The black line corresponds to linear regression in the adaptation phase.

Fig. 5 – Experiment 2: Compensation rates of second saccade amplitude in the post-adaptation phase, per stimulus type and averaged across subjects. Thin lines represent standard deviations.
possibility is that size information about the object is encoded before the saccade and then compared to the post-saccadic object. Adaptation would then be the result of a mechanism that compares pre- and post-saccadic sizes. Since size encoding in the periphery is imperfect, such a comparison mechanism might be useful in that it would compensate for systematic alterations of peripheral vision. Evidence of transsaccadic size information updating has been shown by Vergilino and Beauvillain (2000). They showed that even if the exploring saccade is preplanned as a fixed motor vector, size information guiding an exploring saccade is updated before its execution: they presented a letter string that was shortened or lengthened at different times after the first saccade towards the string and they showed that the saccadic system was able to recalibrate the motor vector of the saccade if the change was intervening very early before the execution of the exploring saccade. This suggests that information about object size may be updated after the first saccade execution and therefore serve in computing the error signal guiding exploring saccade adaptation.

3.2. Plasticity of targeting saccades

In Experiment 2, the second targeting saccade to spatially extended objects was adapted by stepping the whole configuration backward, confirming that the targeting saccade executed between two spatially extended objects is driven by a signal conveying position information.

3.2.1. Absence of transfer to first saccades

Surprisingly, adaptation of the second targeting saccade never transferred to the first saccade of the sequence although their amplitudes were similar. Such a transfer could have occurred since both were targeting saccades, and although the second saccade was volitional and the first reactive, it has been shown that volitional saccade adaptation transfers to reactive saccades (Collins and Doré-Mazars 2006; Alahyane et al. 2007). This suggests that it may be possible to selectively adapt a saccade as a function of its execution rank in the sequence, making saccade rank a context-specific adaptation such as saccade as a function of its execution rank in the sequence. This suggests that information about object size may be updated after the first saccade execution and therefore serve in computing the error signal guiding exploring saccade adaptation.

3.2.2. Information subtending plasticity

Whereas Experiment 2 confirmed that targeting saccade adaptation relies on position information, we showed in Experiment 1 that the adaptation of the exploring saccade partially transferred to targeting saccades aiming for a spatially-extended object and not to those aiming for an isolated target. We propose that this difference is due to the fact that saccades targeting a spatially-extended stimulus are coded not only as a function of stimulus position (like a targeting saccade toward a single target) but also as a function of stimulus size, as they are directed to the center of gravity (e.g. Findlay 1982; Vergilino and Beauvillain 2001). Center-of-gravity calculations by definition have to take object size into account because the borders of the object are crucial to determining the weight of the different elements that drive the motor vector plan. It appears that when object size is a relevant parameter for saccade planning, modifications of size can induce adaptation-like modifications. Following such adaptation mechanisms, all motor vectors that take object size into account are affected, whether they are exploring saccades or targeting saccades to spatially-extended objects. Taken together, our results suggest that plasticity of saccades targeting objects depends on two error signals: one about object position and one about object size.

3.3. Conclusion: Dissociation between targeting and exploring saccades

These two experiments suggest that at least two sources of information can drive adaptation, depending on the relevance of the information for planning the saccade: extrinsic information about object position or intrinsic information about object size. If we consider that saccadic adaptation is a plasticity mechanism allowing saccadic accuracy recovery after extraocular muscle damage, information about object position is most likely to be affected by such damage and therefore to require recalibration. However, it seems that the saccadic system is also capable of taking intrinsic properties such as object size into account to guide its plasticity, perhaps to compensate for errors in encoding object size in peripheral vision.

In conclusion, “purely” targeting saccades based on position information may be adapted by an error signal about the actual landing position of the eye relative to the desired position. Exploring saccades based on object size may be adapted by an error signal comparing the size used for planning with the actual size. This dissociation strongly suggests separate neural mechanisms or substrates involved for these two types of saccades, depending on the information used to compute the movement.

4. Experimental procedures

4.1. Instruments and eye movement recordings

Stimuli were presented on an Iiyama HM240DT monitor with a refresh rate of 170 Hz and a resolution of 800×600 pixels. The experimental sessions took place in a dimly lit room. Subjects were seated 57 cm away from the screen and their head kept stable with a chin and forehead rest.

Eye movements were recorded with an Eyelink® 1000 (SR Research, Ontario, Canada), with a temporal resolution of 1000 Hz, and a spatial resolution of 0.15°. Viewing was binocular but only movements of the right eye were monitored. Each session began with a 9 point calibration over the entire screen. Before each trial, central fixation was checked and compared to the calibration. If the distance between the fixation check and the calibration was greater than 0.75°, fixation was refused and a new calibration was initiated. When successful calibration was detected, the trial began. Online saccade detection corresponded to above-threshold velocity (30°/s) and acceleration (8000°/s²).
4.2. Stimuli

The fixation cross consisted of a 0.5°×0.5° white cross presented 1.8° to 5.0° to the left of screen center. Five different stimuli were presented. They consisted of 0.5°×0.5° white crosses displayed on a dark gray background. Crosses were presented alone, in pairs, or in strings (Fig. 1). We used three different string conditions, all displayed 2.3° to the right of the fixation cross. The single-10X-object and single-12X-object conditions were formed by 10 or 12 adjacent crosses. These single-object stimuli were expected to evoke spontaneous two-saccade sequences, the first saccade landing on the left half of the string and the second on the right half (e.g. Collins et al. 2007b; Lavergne et al. 2008). The two-object condition was formed by 6+5 crosses separated by a 0.5° blank, and was expected to evoke two saccades, one to each string. In addition to the string conditions, the isolated-target condition consisted of a single cross displayed 5.8° to the right, and the isolated-target-pair condition consisted of two crosses, the first 5.8° to the right and the second 3.1° beyond that.

4.3. Subjects

Six subjects participated in Experiment 1 (2 authors and 4 naïve subjects) and four subjects participated in Experiment 2 (1 author and 3 naïve subjects). Subjects of both experiments had normal or corrected-to-normal vision, were familiar with eye movement recording and gave their informed consent prior to starting the experiment, which was carried out according to the ethical standards of the Declaration of Helsinki (2004).

4.4. Procedure and design

Both experiments contained three successive phases: pre-adaptation (150 trials), adaptation (120 trials) and post-adaptation (120 trials) phases. In all phases, a trial began with the display of the initial fixation cross. After a random duration (650–950 ms in steps of 50 ms), the fixation cross disappeared and the stimulus appeared to the right. Subjects were instructed to explore the stimulus without any particular instructions as to the number of saccades to be made.

In both pre- and post-adaptation phases, the stimulus was extinguished upon first saccade detection (see Fig. 1). This extinction was necessary to avoid visual feedback in the post-adaptation phase in which we wanted to measure adaptation retention and transfer. It was also introduced in the pre-adaptation phase in order to obtain an experimentally comparable baseline. The stimulus was randomly and equiprobably one of the five possibilities in the pre-adaptation phase (single-10X-object, single-12X-object, two-object, isolated-target, isolated-target-pair) or one of four in the post-adaptation phase (all except single-10X-object). In all trials, the stimuli evoked either a single saccade or a 2-saccade sequence in which the second saccade was memory-guided.2

2 The term “memory-guided” refers to the fact that second saccades were not visually guided as the stimulus was extinguished during the execution of the first saccade. “Memory-guided” thus designates a methodological procedure here rather than any reference to visual or motor representation stored in memory.

In the adaptation phase of experiment 1, the single-12X-object was presented and then shortened to the single-10X-object upon second saccade detection. In experiment 2, the two-object stimulus was initially presented and then stepped 1° backwards (i.e., towards the fixation cross) upon second saccade detection.

4.5. Data analysis

Overall, 21% of data was excluded in the two experiments (Experiment 1: 19% and Experiment 2: 22%), corresponding to blinks (0.1%), latencies shorter than 100 ms (9%) or longer than 500 ms (0.5%). Conditions in which a two-saccade sequence was expected, trials in which a single saccade (2%), a second regressive saccade (7%) or a third progressive saccade (8.4%) were executed were also excluded from analysis. Overall, 15% of data was excluded for 10X and 12X single-objects; 17% for two-object; 28% for isolated-target-pair stimuli in pre- and post-adaptation phases. 21% and 24% of data were excluded in adaptation phases of Experiments 1 and 2 respectively.

The pre-adaptation phase was the baseline used to quantify adaptation and adaptation transfer, by comparing with adaptation and post-adaptation measurements.

Four conditions evoked a sequence of two saccades (single-10X-object, single-12X-object, two-object, isolated-target-pair) whereas the isolated-target evoked a single saccade. The single-target stimuli were fillers used to prevent subjects from executing stereotyped saccade-sequences on each trial, and we only analyzed data corresponding to conditions in which a two-saccade sequence was induced.

In both experiments, we quantified adaptation by analyzing saccade amplitudes in the condition used to induce adaptation (experiment 1: single-12X-object; experiment 2: two-object) with ANOVAs using Phase (pre-adaptation, adaptation, post-adaptation) as a within-subject factor. For the adaptation phase, only the 30 last trials were considered, in order to have the same number of observations in the three phases. Testing transfer of adaptation to other stimuli conditions consisted of comparing post-adaptation to pre-adaptation values by one-tailed Student t-tests for oriented hypotheses as post-adaptation values were always expected to be lower than pre-adaptation ones. One-tailed t-tests were also used for comparison to standard values (0% and 100%; see results section). We used the same rationale for saccade latencies.

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