Research Report

The use of recurrent signals about adaptation for subsequent saccade programming depends on object structure

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ABSTRACT

Executing sequences of accurate saccadic eye movements supposes the use of signals carrying information about the first saccade for updating the predetermined motor plan of the subsequent saccades. The present study examines the signals used in planning a second saccade when subjects made two successive saccades towards one long or two short peripheral objects displayed before the first saccade execution. Different first eye movement signals could be used: desired eye movement signals, representing the movement necessary for attaining the intended target, or actual eye movement signals, representing the movement actually executed. Experimental dissociation of desired and actual eye movement signals is made possible by adaptive modifications of the first saccade, obtained by transfer of single saccade adaptation, during which the motor vector was progressively modified in response to the systematic intra-saccadic step of a single target. Whether the second saccade used the actual eye movement signal to compensate or not for the adaptive changes in the first saccade depended on which object properties were relevant for saccade planning. Compensation was observed for saccades that aimed for a new object (between-object saccades) because adaptation modifies relative object location. No compensation was observed for saccades that explored an extended object (within-object saccades). Implications for the on-line control of subsequent eye movements are discussed.

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1. Introduction

To accurately direct one's gaze to several objects in visual space, spatial information about the object's image must be converted into motor commands and updated as a function of previous movements. When we look at objects, sequences of saccades, like other voluntary movements, are planned in the brain and depend on intention and selection. It has been proposed that, in the planning of two-saccade sequences, the second saccade computation relies on retinal and extraretinal information indicating the outcome of the first saccade, i.e., the postsaccadic eye position, the intended or the actual eye displacement (Andersen and Gnadt, 1989; Goldberg and Bruce, 1990; Duhamel et al., 1992; Sommer and Wurtz, 2002). However, which eye movement signals about the first saccade are used in the programming of subsequent saccades remains to be determined. The eye movement signals used for on-line control of the subsequent saccade cannot be identified in normal conditions because actual eye movement signals representing the executed movement are similar to desired

eye movement signals representing the eye movement necessary to acquire the target.

Experimental dissociation of these two signals is made possible by saccadic adaptation. In non-invasive adaptation experiments, a repetitive and systematic step of the target during the saccade made to it causes a progressive modification of saccadic amplitude (McLaughlin, 1967). For instance, a gradual decrease/increase of amplitude of primary saccades occurs with a backward/forward intra-saccadic shift of the target. During adaptation, desired eye movement signals coexist with but differ from actual adapted eye movement signals.

A recent study using this saccadic adaptation procedure in which monkeys made two successive saccades towards two briefly flashed discrete targets revealed that the saccadic system had access to precise information regarding the first adapted saccade (Japanese macaques; Tanaka, 2003). When the amplitude of the first of a sequence of memory-guided saccades was adapted, the second saccade took the saccade end position shift into account and corrected its amplitude to accurately reach the second target. Such an updating of the second movement suggests that information about the actual first eye movement, including adaptive modifications, must be relayed to the saccadic system and used for second saccade computation.

It remains unknown whether actual eye movement signals are also used for subsequent movement control in humans. Indeed, while saccadic adaptation exists in both species, important differences exist between humans and macaque monkeys. One of them is the rate of saccadic adaptation, much slower for monkeys (rhesus macaques; Straube et al., 1997) than humans (e.g., Deubel et al., 1986). Furthermore, several studies have provided arguments for selective adaptation in humans, in particular as a function of the way the saccade was elicited. Reactive saccades are stimulus-elicited, i.e., triggered by the sudden display of a target whereas volitional saccades are intentionally generated towards a permanent stimulus. The two types of saccades probably rely on different neural programming circuits (Pierrot-Deseilligny et al., 1995), with a greater implication of cortical processing for the latter. While both volitional and reactive saccades can be adapted, the adaptation of one type of saccade does not transfer (or partially) to the other (Erkelens and Hulleman, 1993; Deubel, 1995; Fujita et al., 2002). More recently, an asymmetric transfer has been reported. The adaptation of volitional saccades was found to transfer well to reactive saccades while the reverse did not occur (Pélisson et al., 2005; Collins and Doré-Mazars, in press).

All these studies suggest that adaptation of volitional and reactive saccades takes place at different sites (Deubel, 1999; Gancarz and Grossberg, 1999). Such selectivity was not found for monkeys who show a robust transfer of adaptation between volitional and reactive saccades (rhesus macaques; Fuchs et al., 1996). These studies indicate critical differences in the cerebral pathways involved in saccade programming.

Several studies in humans have shown that using actual eye movement signals to update a motor plan is not the only operating mode in viewing objects and that movement control depends on the action performed on the objects (Vergilino and Beauvillain, 2001; Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2004). When observers made two-saccade sequences within or between objects that were shifted during the first saccade execution, only second saccades that moved the eye between objects were updated to correct exogenous errors on the first saccade end position. The updating of the second saccade was not found for scanning saccades within objects. These findings reveal a different coding for within- and between-object saccadic eye movements suggesting that such a distinction is a fundamental feature of saccadic planning. While between-object saccades use a retina- or head-centered coordinate system and compensate for the changes in the first saccade end position in order to aim for a precise location in the second object, within-object saccades are coded in an oculocentric coordinate system as a fixed motor vector based on object size and applied irrespectively of the first saccade end position on the object. The absence of an updating suggests that the on-line control of within-object saccades does not rely on actual first eye movement signals.

The goal of the present experiment was to examine which first eye movement signals were used in the second between-object and within-object saccade programming. With a conventional double-step procedure (e.g., Deubel et al., 1986), we adapted a single reactive saccade to modify – by adaptation transfer – the primary reactive saccade of a two-saccade sequence elicited either toward one or two peripheral objects defined by the spatial grouping of individual Xs (Fig. 1A). Because of their length, long strings of Xs used in the one-object condition should be explored by within-object saccades in most cases. Consequently, subjects should execute a two-saccade sequence toward in both object conditions. The first saccade of the sequence was visually guided while the second saccade was memory guided as the stimuli disappeared during the first saccade execution in order to avoid the extinction of the single saccade adaptation. The adaptation of the single reactive saccade was expected to transfer to the primary reactive saccade of the two-saccade sequence directed to the object(s). Indeed, the single target (ST) location corresponded to the majority of first saccade end positions in the two-saccade sequences.[1]

We then examined the effect of first saccade adaptation on second saccade programming.[2] When the primary saccade is

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[1] 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). In this calculation, more weight is given to those elements of the configuration which are closer to the center of the field, resulting in saccade end positions closer to the fovea than the geometric center. Therefore, saccades should be directed toward the center of gravity of each object in the two-object condition. Moreover, the more the peripheral object's size increases, the higher is the probability that a saccade lands on a position nearer to its beginning and that a within-object saccade is executed. Such behavioral patterns are well known in reading research (e.g., McConkie et al., 1989).

[2] Based on previous studies cited in the Introduction that reported no or a partial transfer of reactive saccade adaptation to volitional saccades, we do not expect a transfer of the first saccade adaptation to the second saccade as our procedure elicited a first reactive saccade and a second volitional one.
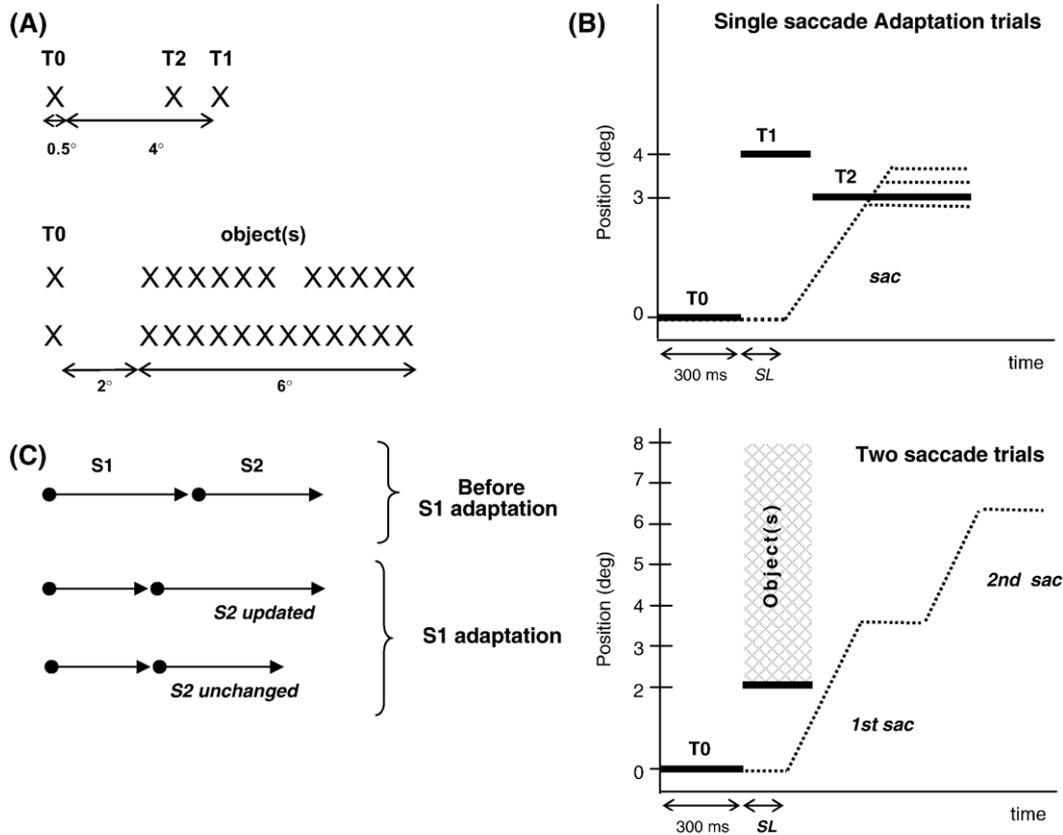
Fig. 1 – Experimental design and hypotheses. (A) Stimuli were crosses 0.5° wide. Simultaneously to the offset of the fixation cross, the single target first stepped 4° right and then 1° left during saccade execution for adaptation trials. Objects used in two-saccades trials were either two short strings of 6 and 5 Xs separated by one space or one long string of 12 Xs. (B) Sequence and timing of target presentation in single saccade adaptation trials and in two-saccade sequence trials. T0: fixation cross, T1: single target and T2: the single target stepped backward during the saccade made to it in the adaptation phase but remained at the same position as T1 in pre- and postadaptation phases (not shown here). SL: saccade latency. The objects were displayed simultaneously to the T0 offset and disappeared during the first saccade execution. No visual stimuli were available for the subsequent saccade. Two-saccade sequence trials were interspersed within single target trials with equal probability in the pre- and postadaptation phases and at low probability in the adaptation phase. (C) Hypotheses on the consequences of backward adaptation of the first saccade (S1) for second saccade (S2) programming. Compared to S2 before S1 adaptation (upper panel), S2 would compensate (middle panel) or not (bottom panel) for adaptation in S1. As a result, S2 end positions should be similar (updating hypothesis) or different (propagation hypothesis) from those before adaptation.

altered by adaptation, the consequences for the second saccade would depend on signals about the first saccade (Fig. 1C). As found by Tanaka in monkeys, we expect that the second saccade would compensate for the adaptive change of the primary saccade (updating hypothesis) suggesting that actual first eye movement signals are used in subsequent saccade programming. The second saccade end positions would not shift relative to the first saccade adaptation. While such predictions could hold for second saccades that aimed for a new selected object, a different pattern is expected for a second saccade that explores an extended object. In this case, the second motor vector would be planned along with the desired first eye movement and would remain identical whatever the adapted state of the primary saccade and applied irrespective of the actual first eye movement end position. In this

case, the second saccade end positions would shift in accordance with the first saccade adaptation (propagation hypothesis).

2. Results

2.1. Result 1: single saccade adaptation transfer to the primary saccade of two-saccade sequences

First saccades showed latencies of about 160 ms, typical for reactive saccades. Statistical analyses were performed on the average individual data of the 54 last trials of the adaptation and postadaptation phases, that were compared to average data obtained in the preadaptation phase (see

Table 1 – Average (±SD) of saccade latency (ms) of the first and the second saccade as a function of trial types (ST, one- and two-object conditions) and phases (preadaptation, adaptation and postadaptation)

	Single target			One object			Two objects		
	Pre	Ada	Post	Pre	Ada	Post	Pre	Ada	Post
Latency									
1st saccade	169±23	162±32	151±39	163±22	164±26	151±34	167±19	164±28	146±36
2nd saccade	–	–	–	307±46	308±45	311±48	323±56	329±57	328±53
Number of:									
Trials	108	648	162	108	108	162	108	108	162
Observations	101±7	604±39	152±10	78±6	82±7	125±11	78±14	83±13	126±12
		[50±4]	[48±6]		[41±6]	[39±7]		[42±7]	[40±5]

Number of trials per subject, average number of observations used for time course and correlation analyses, and average number of observations in [ ] used for analyses of variance on latencies and saccade end position relative change. In these latter cases, only the 54 last trials of the adaptation and post-adaptation phases were taken into account (see text).

Table 1). Such a partitioning allowed to limit analyses to trials which clearly differentiated the three phases. Analyses of variance showed that the average saccade latency did not differ between ST, one- and two-object conditions ($F<1$) and phases ($F(2,10)=1.86$, NS). These two factors did not interact ($F<1$).
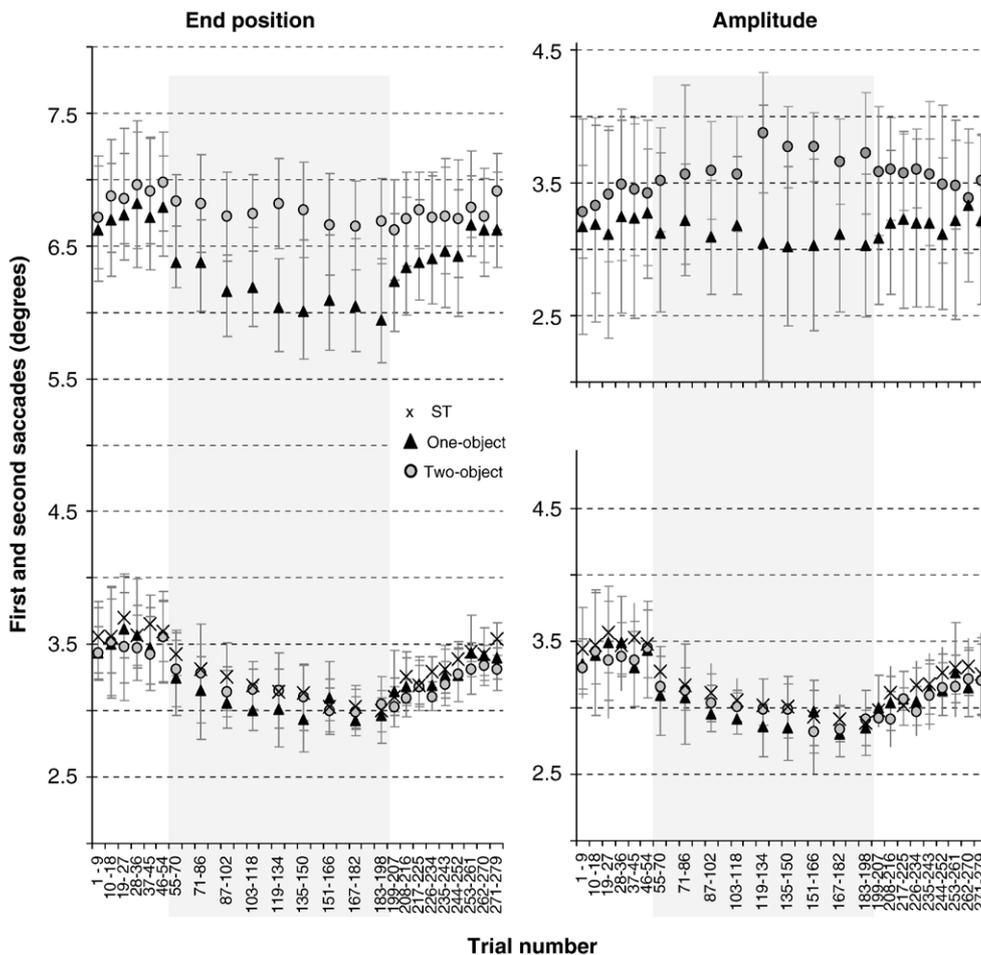

Fig. 2 – First saccade end positions (left panel, lower curves) and amplitudes (lower right panel) for ST, one- and two-object trials (crosses, triangles and circles respectively), second saccade end positions (left panel, upper curves) and amplitudes (upper right panel) for one- and two-object trials, for the three successive phases. Each point represents the average over the six subjects. Errors bars are ±SD. Note that there were 9 successive trials per bin in the pre- and postadaptation phases (each trial rank was tested twice per subject and per condition) and 16 successive trials per bin in the adaptation phase (per subject, each trial rank was tested 4 or 5 times for the ST condition and 12 out of the 16 ranks were tested once for each object condition). The different bin sizes resulted from the different ratios between ST, one- and two-object trials in the different phases. The grey zone indicates the adaptation phase (ST backward step for trials 55 to 198).

The time course of the first saccade end position in single target, one- and two-object trials can be seen in Fig. 2 (left panel, lower curves). For each subject, each phase and each stimulus condition (ST, one- and two-objects), we calculated the average of the first saccade end position for bins of successive trials. Each point represents the average (and SD) of the six subjects The size of the bins was not constant across phases as the ratio of ST and object trials differed between the pre- and postadaptation (1/3 of each) phases compared to the adaptation phase (6/8 ST, 1/8 1OB, 1/8 2OB). The preadaptation phase (trial ranks 1 to 54) was divided into 6 bins of 9 ranks and the postadaptation phases (ranks 199 to 279) into 9 bins of 9 ranks, for each stimulus condition. The adaptation phase (trial 55 to 198) was divided into 9 bins of 16 ranks. Table 1 indicates the number of trials and observations for each condition.

During the preadaptation phase, first saccade end positions were similar between single and two-saccade sequences, even if single saccades slightly undershot the single target. As expected from previous studies in humans, subjects progressively reduced the size of their saccade when the backward step of the ST was introduced. Time courses of the first saccade end positions showed a similar backward shift in both one- and two-object conditions. Once the single target did not step backwards anymore (postadaptation phase), a progressive extinction of adaptation was observed for the single saccade as well as the first saccade of the two-saccade sequence. As expected, the modification of the first saccade that aimed for an object occurred concurrently with the adaptation of the single saccade induced by the systematic backward step of the single target. Note that the same pattern was found on first saccade amplitude (Fig. 2, lower right panel).

Fig. 3 presents the average relative saccade end position change[3] in adaptation and postadaptation phases compared to the preadaptation phase. Only the last 54 trials of the adaptation and postadaptation phases were taken into account for analyses of variance. Regarding the first saccade (left panel), there was a significant effect of the phase ($F(1,5)=50.91$, $P<0.001$): compared to the preadaptation phase, we observed a 60% change for ST saccades in the last trials of the adaptation phase and an almost complete extinction of adaptation in the postadaptation phase where the single target did not step backwards (13.5% change, not statistically different from 0, Student T-test, $t_{[5]}=2.26$, NS).When saccades to the single target were adapted, we observed a similar change of end positions of the first of the two-saccade sequence (52% and 45% change for one- and two-object conditions ($F(1,5)=3.36$, NS). No significant difference between ST and object conditions ($F(2,10)=1.08$, NS), and no interaction with phase were found ($F(2,10)=1.73$, NS). Furthermore, the extinction of ST adaptation at the end of the postadaptation

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[3] The adaptive change of saccades can be assessed by the absolute difference between saccade end positions observed in the adaptation (or postadaptation) and those observed in the preadaptation phase. The relative change of saccade end positions is obtained when the difference between preadaptation and adaptation (or postadaptation) is related to the step size. This provides the amount of step size compensation (e.g. a 100% relative change corresponds to full compensation of the target step).
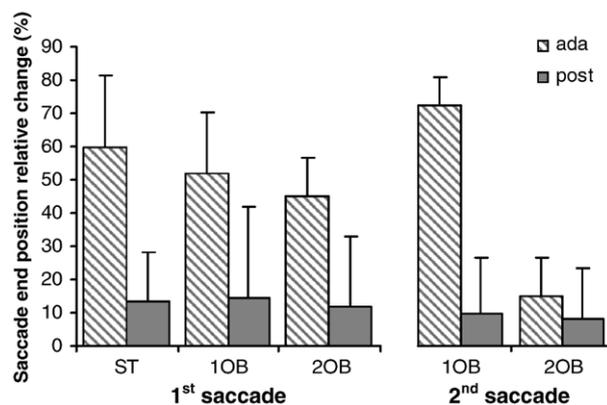

Fig. 3 – Average relative change (%) of the first saccade end position (left) for single target (ST), one-object (1OB) and two-object (2OB) trials and of the second saccade end position (right) for one- and two-object trials. Positive values indicate a shift in the direction of the ST step (backward). Only the last 54 trials of the adaptation and postadaptation phases are taken into account. Average change of each bin was calculated using the formula: [(preadaptation end position – adaptation (or postadaptation) end position)/1° step size]. Error bars are ±SD.

phase was accompanied by a decrease in saccade end position changes, similar for one- and two-object conditions ($F<1$), revealing that first saccades landed on a position near to that observed in the preadaptation phase (15% and 12% change respectively, not different from 0, Student T-tests, $t_{[5]}=1.39$ and $t_{[5]}=1.27$, NS).[4]

Adaptation transfer is the ratio between the amount of change of the first saccade of the two-saccade sequence and that of the single saccade. As can be inferred from Fig. 3, when the final trials of the adaptation phase averaged across subjects were considered, a transfer of adaptation was found for first saccades in both object conditions (87% and 75% for one- and two-object conditions). No significant transfer differences between object conditions and between phases (adaptation and postadaptation), and no interaction between the two factors were found ($Fs<1$).

2.2. Result 2: selective compensation of primary saccade adaptation by the second saccade

In the course of first saccade backward adaptation, we observed a concomitant leftward shift of the second saccade end position in the one-object condition while the second saccade end positions remained relatively stable in the two-object condition (Fig. 2, left panel, upper curves). Accordingly, an inverted pattern was found for the second saccade it (Fig. 2, upper right panel): the amplitude in the one-object condition

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[4] In the present study, only the visual structure of stimuli differentiated the two- from the one-object condition. In the peripheral Xs string, removing the seventh X was sufficient for perceptual processing of individual Xs as either a long object or two successive short objects and for different second saccade programming.

remained relatively stable across phases while it changed as a function of the adapted state of the first saccade in the two-object condition.

In order to quantify the compensation of the primary saccade adaptation by the second saccade, the percent change in the second saccade end position was calculated as the difference between adaptation (or postadaptation) and preadaptation relative to step size, as defined in Section 2.1 (Fig. 3 right). If the second saccade compensated for the adaptation of the first, then we would expect no change of the second saccade end position during the adaptation phase (updating hypothesis). If the second saccade did not compensate for the adaptation of the first, then we would expect a change of the second saccade end position mirroring the adaptive modification of the first saccade (propagation hypothesis). ANOVA indicated that both phase and object condition affected the relative change of the second saccade end position ($F(1,5)=33.50$, $P<0.002$ and $F(1,5)=113.3$, $P<0.003$, respectively). More interestingly for our purpose, there was an interaction between object condition and phase ($F(1,5)=47.14$, $P<0.001$). In the adaptation phase, the end position change was greater for the one-object than for the two-object condition ($F(1,5)=255.21$, $P<0.0001$). No effect of object conditions was found in the postadaptation phase ($F<1$), and the percent changes in this phase were not different from 0 (10% and 8%, Student T-tests, $t_{[5]}=1.63$ and $t_{[5]}=1.07$, NS) indicating the near complete extinction of adaptation. Furthermore, the effect of phase was significant for the one-object condition ($F(1,5)=75.99$, $P<0.0005$) but not for the two-object condition ($F(1,5)=1.14$, NS).

The analysis of the relationship between first and second saccade end position (Ditterich et al., 1998) is another convincing argument for the presence or lack of second saccade compensation. The updating hypothesis predicts that the second saccade should compensate for the adaptive modification of the first saccade end position. A total compensation should give a slope of 0 for the regression function of the analysis, the second saccade end position being unaffected by the first saccade end position change. However, previous studies (Vergilino and Beauvillain, 2001; Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2004, 2006) have shown that the between-object saccade did not target a precise fixed location but was directed towards the center of gravity of the remaining stimulation beyond the first end position. In this case, the slope of the regression function is close to 0.5. Alternatively, the propagation hypothesis predicts that changes of the first saccade end position resulting from adaptive modifications should spill over to second saccade end positions. In such a case, the slope of the regression function should be close to 1.

Fig. 4 shows the relationship between first and second saccade end positions plotted for each subject, with the three phases pooled. All subjects except one (S5), presented a difference in the slopes of the regression function between the one- and two-object conditions. The individual slopes were close to 1 for the one-object condition and between 0 and 0.5 for the two-object condition. The analysis of variance revealed an effect of the object condition (average slopes of 0.8 ± 0.1 and 0.5 ± 0.1 for the one- and the two-object conditions respectively, $F(1,5)=41.76$, $P<0.001$).

Furthermore, second saccades that compensated or not for the first saccade adaptive change also differed as to their latencies (Table 1). Analyses of variance based on the last 54 trials of the adaptation and postadaptation phases revealed that the second saccade latencies in the two-object condition were longer than in the one-object condition ($F(1,5)=10.26$, $P<0.02$). There was no effect of the phase and no interaction between these two factors ($Fs<1$). The second saccade latencies differed between the one- and the two-object conditions, suggesting that the updating mechanism occurring after the first saccade for the two-object cases is a time-consuming process. Such a result reinforces the idea that the programming of within-object saccades differs from the between-object saccades.

3. Discussion

The major finding of this study is that, after the adaptation of the first saccade obtained by transfer, the second saccade of the sequence compensated for the adaptive change only when this second saccade aimed for a new object. When it explored the same object, there was no updating of the second saccade with respect to the adaptive changes of the first saccade. Instead, the adaptive change of the first saccade was propagated to the second saccade.

3.1. On the adaptation transfer

In the course of single saccade adaptation, the systematic backward step of the single target led to the reduction of saccade amplitude. The single saccade adaptation transferred to the primary saccade of two-saccade sequences directed towards one or two extended objects. Such a transfer was expected for several reasons. Because of the selective nature of saccadic adaptation in humans, we examined first saccades in the two-saccade sequences that shared many characteristics with the single saccades. Both had similar amplitudes and were in the same direction. Such parameters are crucial to assure transfer (Deubel et al., 1986), as the amount of transfer decreases the more the amplitude of saccades differs from that of the adapted saccades (Noto et al., 1999 in rhesus macaques; Semmlow et al., 1989 in humans). In addition, both single saccades and primary saccades of the two-saccade sequence were reactive saccades, i.e., elicited by the appearance of the peripheral stimulus. Such a precaution was also crucial as no or partial transfer was found between reactive and other volitional (memory-guided) saccades such as those elicited for second saccades in this study (Deubel, 1995; Fujita et al., 2002).

3.2. On the selectivity of the second saccade updating

The present study demonstrates that the second saccade of a two-saccade sequence compensated for the changes in the first saccade end position only when the second saccade aimed for another object (updating hypothesis). In this case, a specific location in the second object is selected as the second saccade target and the adaptive changes of the first saccade lead to modifications of the second saccade to aim for that
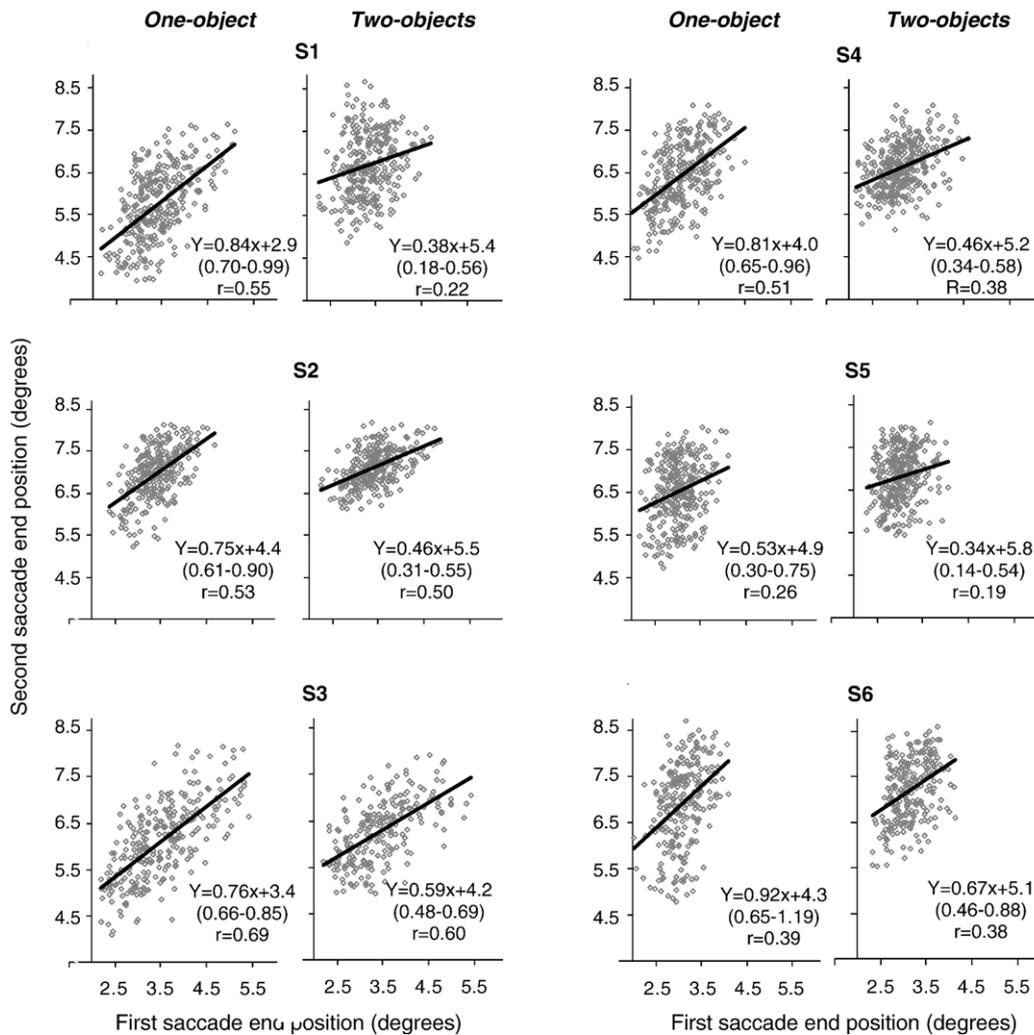
Fig. 4 – Individual correlation between the first and second saccade end positions (in degrees) for the one-object and two-object conditions (respectively left and right panel for each subject). The 95% confidence intervals for the slope are given in parentheses. All correlation coefficients (r) are positive (Ps < 0.025).

target location in the second object. Indeed, the second saccade end position into the second object did not change as adaptation modified the first saccade. A very different pattern of results was found for within-object saccades for which different second saccade end positions were observed as a function of the adapted state of the first saccade (propagation hypothesis).

Our present results suggest that saccade programming uses the actual eye movement signals when the goal of the subsequent movement is to acquire a new object. As found previously in macaque monkeys performing a two-saccade sequence towards two isolated targets (Tanaka, 2003), the second saccade planning takes into account the first saccade change, suggesting that actual first eye movement signals are used by the saccadic system to program subsequent movements. Our results provide evidence that the human saccadic system also uses signals downstream from the site of saccadic adaptation in order to keep saccade targeting precise. Interestingly, the perceptual system also seems to use the actual eye movement signal. Visual attention is directed towards the location the eyes are aiming for, as shown by behavioral

studies in which relative perceptual performance across the visual field is taken as an indicator of the focus of visuo-spatial attention (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Doré-Mazars et al., 2004). Furthermore, the focus of attention shifts with saccadic adaptation, suggesting that signals downstream from adaptation (representing actual movement) were also used by the perceptual system (Doré-Mazars and Collins, 2005). The orientation of attention seems therefore to be tied to the end position of the to-be-executed saccade vector, and not to the desired presaccadic target. This reinforces the claim that the perceptual system must have access to precise information regarding the next movement, as the saccadic system does (Tanaka, 2003; Sommer and Wurtz, 2002). If the same actual signal is used by both systems and contributes to accurate action and perception, the specific updating of the second eye movement for between-object saccades found in the present study suggests that the object selection process is crucial for the subsequent action and for perception.

Finally, the present data show that the saccadic system does not use the actual eye movement signal when the second

saccade explores the same object. In agreement with previous studies that have shown that such a saccade did not take into account exogenous errors induced by different shifts of the object during the first saccade (Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006), we did not observe here an updating of the second saccade as a function of the adapted state of the first saccade, suggesting that there is no precise target position for the second saccade. Rather, the saccade was coded as a fixed motor vector applied irrespectively of the initial saccade end position on the object. Thus, the second saccade does not compensate for first saccade end position alterations, whatever the source, exogenous with contingent displacement or endogenous with adaptation. This is in accordance with previous studies showing that the exploration of an extended object relies on a preplanning of the saccade sequence in which object size is the primary determinant of second vector computation. Within-object saccades are planned before the first saccade execution and associated with a specific desired first saccade end position (McDonald and Shillcock, 2004; Vergilino-Perez et al., 2004; McDonald and Vergilino-Perez, 2006). However, the present experiment provides a new insight about the specific coding of within-object saccades. Indeed, despite the modification of the internal state of the motor system, the second saccade directed within the same object does not consider extraretinal feedback about the actual eye position after the first saccade.

Our results clearly show that signals about the first saccade adaptation play a role in the programming of the subsequent eye movement only when a precise location is selected within an object. The asymmetry observed in the use of signals may be explained by the different coordinate systems involved in the planning of between- and within-object saccades. A representation in an object-centered reference frame (Olson and Gettner, 1995; Olson, 2003) can be first used in the planning of saccades towards a specific part of the selected object. Such a representation would come into play at the time of the saccade target selection and then involve recruitment of egocentric coordinate system (retina- or head-centered) to execute the saccade (Goldberg and Bruce, 1990; Duhamel et al., 1992; Xing and Andersen, 2000). In this case, the system uses the actual first eye movement to update the second target location for the second saccade. Alternatively, saccades that explore an extended object involve a representation in motor coordinates specifying the direction and the amplitude of the movement, coded before the execution of the first saccade, and not updated. Oculocentric motor representations that specify the amplitude of the eye movement have been found in different cerebral areas, but the activity of neurons is observed before the execution of the second saccade (Sparks, 1986; Gnadt and Andersen, 1988; Goldberg and Bruce, 1990). In humans, neural systems that mediate our ability to execute saccades in different reference frames are not well understood. Nevertheless, object selection processes determine the signals used for the updating of subsequent eye movements.

4. Conclusion

Overall, this study gives additional support to the hypothesis of different coding for eye movements according to their goal,

using specific object properties. We propose that the updating of a saccade would occur when information useful for its coding are affected. A specific updating, reflected by the flexibility of the motor vector, occurs for between-object saccades probably because saccadic adaptation causes modifications in the relative spatial location of the object. Because saccades that aim for a new object need information about relative spatial location to aim for a precise target position, all modifications regarding first saccade end position are compensated for in order to finally reach that selected target. On the contrary, saccades that explore the same object depend on its intrinsic spatial properties such as size. The absence of an updating of the second saccade in this case could be the result of the fact that adaptation does not affect size information. In other words, the eye movement signals used in the planning of sequences of saccades depend on which information about the object is affected and which information is used to plan the subsequent action.

The saccadic system includes adaptive mechanisms that maintain saccade accuracy throughout life, in spite of developmental and pathological changes (e.g., Munoz et al., 1998). Thus maintaining precision requires mechanisms capable of evaluating errors and adapting future behavior accordingly. Without such mechanisms, there would be a constant discrepancy between the goal and the movements made to attain it. Our study supports this view but also suggests that when a saccade within a spatially extended object is programmed, correct aiming is no longer as crucial because the movement is exploratory rather than goal directed. Thus, adaptive mechanisms designed to maintain correct targeting would not need to be applied to these saccades.

5. Experimental procedures

5.1. Subjects

Two authors and four naïve subjects participated in the experiment. All six subjects were familiar with eye movement experiments.

5.2. Materials and apparatus

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[5]. Signal from the oculometer was sampled every 2 ms. The beginning and end of a saccade were detected by the time

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[5] Adaptation is thought to occur conjugately for both eyes in humans (see Hopp and Fuchs, 2004 for a review).

derivative of the voltage signal sampled by the eye tracker and the graphics interface that control 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).

The visual stimuli were green Xs on a black background, and their apparent luminance of each was set at 0.40 cd/m^2 at the beginning of each session with a Minolta LS-110 luminance-meter. Each X was 0.5° wide. In single target trials, the target was an X displayed at 4° to the right. In one and two-object conditions, 2° to the right, a 6° wide peripheral string of Xs was presented horizontally, twelve Xs or six and five Xs separated by a blank, respectively (Fig. 1A).

5.3. Experimental procedures

At the beginning of the session, the eye position on the screen was calibrated by requiring the subjects to sequentially fixate five vertical bars, 3° apart, arranged 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, and if necessary, a new calibration was performed. When the computer detected an accurate fixation on the left calibration bar, this bar was replaced by the fixation target (T0), and the next experimental trial began. The eye movement was recorded throughout the whole trial. Finally, a check of the eye position was done during the T0 display. The trial was canceled if the eye position deviated more than 0.5° from T0 center.

Each subject performed six sessions (279 trials in each session) on different days. Before the first session, subjects ran 45 trials that had the same characteristics as preadaptation trials but no particular training was required to make two-saccade sequences.

5.3.1. Single target adaptation procedure
After fixation of the stationary target (T0) for 300 ms, target T1 appeared 4° to the right. The appearance of T1 was the signal to move the eyes toward it. During adaptation trials, T1 was shifted 1° to the left during the saccade made to it causing a postsaccadic error and remained there until the end of the trial (Fig 1B). The target stepped when the eye crossed an invisible boundary located 1° to the right of the fixation cross (T0). In pre- and postadaptation phases, T1 appeared in exactly the same way as in adaptation phase but did not step during saccade execution. Subjects were required to make a single saccade toward the isolated X and then to press a button in order to trigger the next trial.

5.3.2. Procedures specific to within- and between-object saccades
In the one- and two-object conditions, the objects were constituted of one or two strings of Xs. The first saccade was visually guided while the second saccade was memory guided. Indeed, the stimuli disappeared during the first

saccade execution, after the eye crossed an invisible boundary located 1° to the right of the fixation cross (T0) (Fig. 1B). The task of the subjects was to explore the objects as if they were always displayed on the screen. Then, the subjects had to press a button to trigger the next trial.

For each session, in pre- and post adaptation phases, consisting of 54 and 81 trials respectively, one- and two-object trials were interspersed with equal probability within single target (ST) trials (33% for each condition). The adaptation phase consisted in 144 trials in which object trials were interspersed at low probability (12.5% and 12.5% respectively for one and two-object conditions) within the ST trials (75%), in order to maintain the adapted state of the primary saccade.

5.3.3. Data elimination
Overall, a small proportion of the data were discarded because the eye movement measurement was inaccurate or interrupted by blinks (4%), the first saccade end position was more than 2 standard deviations from the average (11%), or the first saccades were predictive or premature (latency < 50 ms) (4%). In addition, for both object conditions, sequences of single or three or more saccades were not taken into account (respectively 7 and 5%).

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