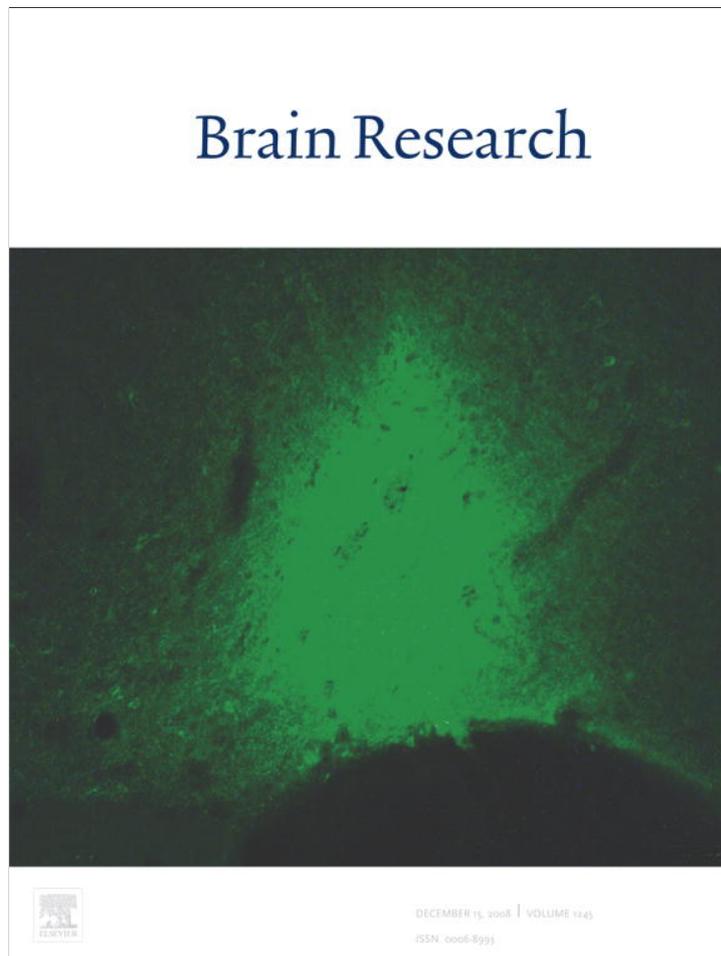


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Research Report

The planning of a sequence of saccades in pro- and antisaccade tasks: Influence of visual integration time and concurrent motor processing

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ABSTRACT

Previous studies have shown that a saccade is coded in a specific reference frame according to its goal: to aim for a new object or to explore an object which has already been fixated. In a two saccade sequence, the second saccade aiming for a new object is programmed in a retinocentric reference frame in which the spatial location of the second object is stored in spatial memory before the first saccade and updated after its execution. The second saccade exploring the same object is coded in an oculocentric reference frame in which object size is directly transformed into a fixed motor vector, encoded in motor memory before the first saccade and simply applied after its execution. The integration of parafoveal visual information appears to be crucial in the selection of the appropriate reference frame. The two experiments presented here investigate how and when the saccadic system integrates visual information to plan a sequence of saccades. In separate blocks, subjects were asked to execute a sequence of prosaccades directed toward a single object or two short objects, or to execute a sequence of antisaccades in the opposite direction of the stimuli. The latency of the initial saccade was modulated by using the Gap-200, Gap-0 and Overlap-600 ms paradigms. The results show that the time available for segmenting the visual stimulation into discrete objects and application of a specific reference frame according to this segmentation is critical for saccadic planning.

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1. Introduction

In order to explore the visual environment, observers plan and execute rapid eye movements called saccades that shift gaze from one fixation point to another. Visual information initially available in retinal coordinates must be transformed into motor commands through a series of operations known as sensorimotor transformations. In the laboratory, the majority of studies that examine saccadic planning focus on single saccades that shift gaze from one simple target, like a short

duration dot, to the other. For such saccades, the saccadic vector might be computed directly from the retinal coordinates of the target, defined by the eccentricity between the actual eye position and the target location. However, our visual environment is full of spatially-extended objects and in many real-life tasks, such as reading or scanning a visual scene, the observer executes saccade sequences, some saccades shifting the gaze to a new object and others shifting the gaze elsewhere in the same object. Previous studies have identified the relevance of this distinction (based on the action

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to be performed) for saccade planning (e.g. Vergilino and Beauvillain, 2001; Vergilino-Perez and Findlay, 2003; Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006). By contrasting the second saccade as a function of the action goal – to aim for a new object or to explore the same object – the authors showed the use of specific reference frames for each action. Within-object saccades were coded in an oculo-centric reference frame as a fixed motor vector applied irrespective of the initial landing position on the object. The second saccade motor vector was planned before the execution of the first saccade and computed as a function of the object size integrated in the periphery: the longer the object, the longer the size of the motor vector (Vergilino and Beauvillain, 2000). The sensorimotor transformation processes for the second saccade occur before the execution of the whole sequence, the within-object motor vector being encoded in a motor memory during the execution of the first saccade. Alternatively, between-object saccades would be coded in a retinocentric reference frame in which the second object location is encoded in spatial memory before the execution of the first saccade and updated afterward as a function of the new eye position. Therefore, the sensorimotor transformation for the second saccade occurs after the execution of the first saccade. The updating process during fixation on the first object can explain why between-object saccade latencies are longer than within-object saccade latencies. Overall, these studies showed that the goal of the action determines which spatial information – the location or the size of the object – is relevant for saccadic planning. Therefore, the visual information relative to the structure of the peripheral stimuli appears to be crucial in the selection of the appropriate reference frame. The question then arises as to whether the use of a specific reference frame for second saccade planning (oculo-versus retinocentric) depends on the time available for the integration of peripheral visual information before the execution of the saccade sequence.

A great number of studies have demonstrated that information presented before first saccade onset can be used to drive the second saccade (e.g. Becker and Jürgens, 1979; Findlay and Harris, 1984; Aslin and Shea, 1987; Walker and McSorley, 2006). For example electrophysiological evidence for temporal overlap of first and second saccade planning was provided by a study measuring the neural activity in monkey superior colliculus, and showing that for fast sequences of saccades, motor activity related to the second saccade goal increased before first saccade onset and was maintained during its execution (McPeck and Keller, 2002). Also, the time course of visual information accrual that guides the first and second saccades in a visual search task was examined (Caspi et al., 2004). The results revealed that visual information was being accumulated simultaneously for the first and the second saccade before the execution of the first saccade. Integration of visual information for the planning of the second saccade begins after integration of visual information for first saccade planning but continues during the first saccade's dead time (i.e. the interval time immediately preceding the saccade execution during which metric changes can no longer be obtained).

In Vergilino-Perez and colleagues' work, parallel planning of saccades depended on the visual object structure obtained in parafoveal vision and on the action to be performed on the

object (to aim for a new object or to explore the same object). It is possible that the coding of saccade sequences in specific reference frames depends on the time interval available before first saccade onset, during which parafoveal visual information can be extracted and used to guide action planning. Because the natural variability of the first saccade latency is not large enough to examine this question, we chose to decrease or increase it with the use of the gap and overlap paradigms (Saslow, 1967). The introduction of a gap period without any stimulation reduces the latency of the saccade, up to "express" saccades with latencies around 100 ms (Fischer and Breitmeyer, 1987). On the contrary, in the overlap paradigm, the foveal fixation cross and the target stimulus remain present together on the screen, the extinction of the cross being the start signal for the saccade. Mean latency is around 220 ms (Becker, 1989). In the present experiments, we used Gap-200, Gap-0 and Overlap-600 ms procedures in order to examine the role of the time available for parafoveal visual integration in the planning of two-saccade sequences.

Another way to manipulate the time available for saccade preparation is to load the saccadic system with additional processes that have to be carried out in conjunction with motor planning. The antisaccade task, in which subject were required to make an eye movement away from a visual target, involves such supplementary processes. The system has to first inhibit the reflexive prosaccade toward the visual target and then to program the voluntary antisaccade to the opposite direction (see Munoz and Everling, 2004 for a review). These supplementary processes could explain why antisaccade latencies are longer than prosaccade latencies. In the two experiments described here, we examined sequences of two pro-or anti-saccades in order to investigate whether the reference frames involved in saccade sequence planning are preserved when concurrent processes are involved during saccade planning.

The experiments presented here examined the coding of a sequence of two saccades, the second saccade being directed to a new object or within the same object (see Fig. 1, left panel). The total length of the stimuli could be of 10 or 12 crosses and for one total length, the single long object or the two separate objects both occupied the same space. Three delays of presentation of the objects in periphery were introduced: a Gap-0 and an Overlap-600 ms delay in Experiment 1 and a Gap-200 ms delay in Experiment 2. With gap paradigms, the time interval available for sequence planning is the first saccade latency, whereas with the overlap procedure, the saccadic system should benefit from additional 600 ms to encode the visual stimulation and plan the saccades. For both experiments, we examined two saccade sequences in both prosaccade and antisaccade tasks, in separate sessions.

For the prosaccade task, we expected that the two-saccade sequence would be planned in a specific reference frame according to the action (to aim for two separate objects or to explore the same object) in both Gap-0 ms and Overlap-600 ms (Exp1), as previously found with similar procedures (e.g. Beauvillain et al., 2005). The motor planning of a two-prosaccade sequence has never been tested with a Gap-200 ms delay (Exp 2). It is possible that in this time-pressured situation the saccadic system would not have enough time to encode the visual stimulation and plan the sequence in a

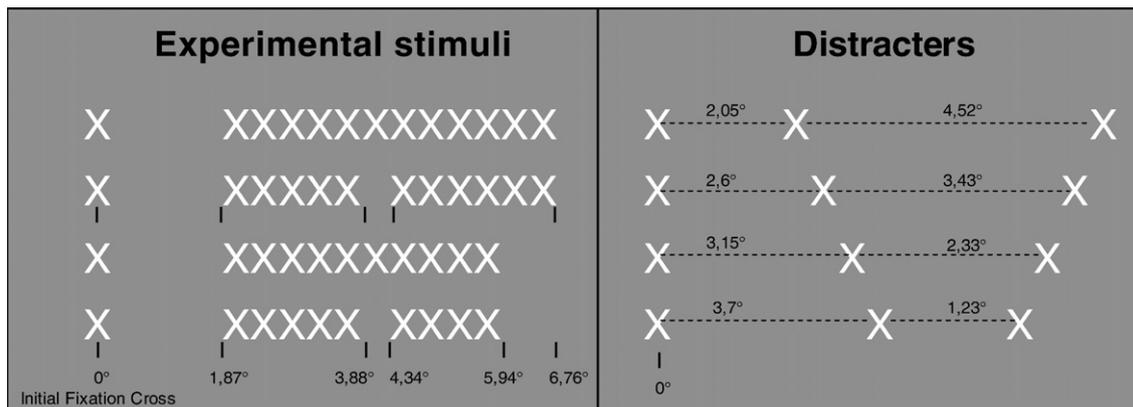


Fig. 1 – Examples of stimuli. The initial fixation cross is always displayed in the center of the screen whereas the stimuli can be presented to its right (as shown here) or its left. The left panel presents the experimental stimuli. The series of crosses constituted either a single long object of 10 or 12 crosses or two separate objects. In the two-object conditions, the first object was always constituted of 5 crosses followed by a second group of 4 or 6 crosses. The numbers (not presented during the experiment) indicate the beginning and the end position of each object on the screen in degrees. The right panel presents the distracters, and gives the eccentricity in degrees between the initial fixation cross and the first distracter as well as between the first and the second distracter.

specific reference frame. Moreover, with the antisaccade task, we investigated the use of specific reference frames when concurrent processes occurred. We expected that both might interact, i.e. the load due to antisaccade planning and the shortening of the available preparation time would critically damage the specific planning of the two-saccade sequence.

2. Experiment 1

In the first experiment, we examined the coding of a sequence of two prosaccades or two antisaccades executed when a single long object or two separate objects were presented. In the one-object conditions, the object length could be either of 10 or 12 crosses whereas in the two-object conditions, the first object was of 5 crosses followed by a 4- or a 6-cross object. We modulated the time interval available for the planning of the saccade sequence by using Gap-0 and an Overlap-600 ms paradigms.

2.1. Results

2.1.1. First saccade of the two-saccade sequence

2.1.1.1. Latencies. Table 1 shows that mean first saccade latencies were significantly longer in the antisaccade task than in the prosaccade task (respectively, 283 ms versus 193 ms, $F(1,6)=19.64, p<.005$). Latencies in the Gap-0 were not significantly different from those in the Overlap-600 condition ($F<1$). There was no interaction between the preparation time (i.e. Gap-0 versus Overlap-600) and task (pro-versus antisaccades) ($F<1$). Finally, the effects of the number of objects (one versus two), the length (10 crosses versus 12 crosses) and the side of object presentation (left versus right) were not significant ($F_s<1$ for object number and length: $F(1,6)=2.24$ ns for side of the object presentation).

2.1.1.2. Landing positions¹. First saccade landing positions were farther into the object in the prosaccade condition relative to the antisaccade condition (2.8° versus 4.1°) although the difference failed to reach significance ($F(1,6)=4.13, p<.08$). No other factor significantly influenced landing positions ($F_s<1$ for preparation time, number of objects, side of the object presentation and $F(1,6)=2.83$ ns for object length).

2.1.2. Second saccade of the two-saccade sequence

2.1.2.1. Relationship between the first and second saccade landing positions. The coding of the second saccade can be investigated with regression functions relating first and second saccade landing positions, as introduced by Ditterich et al. (1998). In a retinocentric reference frame, the spatial location of the second object is updated after the first saccade relative to the new eye position to aim for a specific target location on the second object. We then expect a slope of 0 between first and second saccade landing positions, indicating that second saccade landing position is unaffected by the first saccade landing position. However, previous studies have shown that the second saccade does not target a precise fixed location but is directed rather to the centre of gravity of the remaining stimulation beyond the first landing position, giving a slope close to 0.5 (Vergilino and Beauvillain, 2001; Beauvillain, et al., 2005; Vergilino-Perez and Findlay, 2006). Alternatively, an oculocentric reference frame involves the planning of a fixed-motor vector applied irrespective of the initial fixation on the

¹ The landing position reported here corresponds to the final eye position of the primary saccade, expressed in degrees relative to the center of the screen that is noted by convention 0° . We did not observe small corrective eye movements, probably as we did not ask explicitly the subjects to aim for a precise location on the objects.

Table 1 – Experiment 1

	Gap-0 ms								Overlap-600 ms							
	1 object (1OB)				2 objects (2OB)				1 object (1OB)				2 objects (2OB)			
	10 crosses		12 crosses		5+4 crosses		5+6 crosses		10 crosses		12 crosses		5+4 crosses		5+6 crosses	
	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left
<i>Prosaccades</i>																
1st sac latency (ms)	174	180	171	185	170	177	168	181	212	217	214	201	213	206	207	220
	28	28	21	32	17	30	19	27	60	57	50	49	53	50	40	63
1st sac landing position (°)	2.8	2.8	2.7	2.9	2.8	2.9	2.8	2.9	2.8	2.4	2.8	2.4	3	2.7	3	2.6
	0.5	0.6	0.4	0.6	0.4	0.5	0.4	0.5	0.5	0.4	0.6	0.4	0.4	0.4	0.4	0.3
2nd sac latency (ms)	280	298	270	286	307	319	309	344	329	376	322	382	403	432	423	433
	84	96	85	90	88	121	81	119	57	81	65	81	96	128	123	146
2nd sac landing position (°)	5.5	5	5.9	5.4	5.3	5.1	5.7	5.5	5.3	4.7	5.8	5.2	5.5	4.8	5.9	5.3
	0.4	0.6	0.5	0.7	0.4	0.5	0.5	0.5	0.7	0.7	1	0.7	0.3	0.4	0.3	0.6
2nd sac amplitude (°)	2.6	2.2	3.2	2.5	2.4	2.2	2.9	2.6	2.6	2.3	3.1	2.8	2.4	2.1	2.9	2.6
	0.7	0.8	0.8	0.9	0.6	0.7	0.8	0.8	0.9	0.9	1.3	1	0.5	0.7	0.6	0.8
LP1/LP2 slope of regression function	1.18	0.71	1.34	0.90	0.68	0.49	0.61	0.48	0.84	0.90	1.07	1.16	0.64	0.64	0.74	0.69
	0.6	0.3	0.5	0.3	0.2	0.3	0.4	0.4	0.5	0.3	0.3	0.3	0.3	0.4	0.3	0.4
<i>Antisaccades</i>																
1st sac latency (ms)	273	275	284	270	275	274	276	274	301	296	300	278	291	280	294	280
	58	48	58	50	51	49	57	51	151	147	146	123	156	137	142	130
1st sac landing position (°)	4.1	4.3	4.1	4.2	3.8	4.2	4.2	4.3	4.1	4.4	4	4.5	3.7	4.2	3.8	4.5
	1.6	1.9	1.5	1.6	1.2	2	1.7	2	1.9	2.4	1.3	2.6	1.6	2.4	1.2	2.3
2nd sac latency (ms)	281	279	276	284	289	289	288	308	281	279	276	284	289	289	288	308
	38	50	49	36	44	51	56	55	38	50	49	36	44	51	56	55
2nd sac landing position (°)	5.7	6.4	5.9	6.5	5.6	6.3	5.9	6.6	6.1	6.5	6.2	7.1	5.7	6.6	5.9	7.1
	1.7	1.9	1.6	1.4	1.4	1.9	1.8	1.8	1.9	2.6	1.4	2.8	1.5	2.8	1.5	2.9
2nd sac amplitude (°)	1.6	2.1	1.8	2.3	1.8	2.1	1.7	2.3	2	2.2	2.2	2.6	2	2.4	2.2	2.6
	0.4	0.4	0.4	0.3	0.4	0.4	0.6	0.3	0.5	0.4	0.5	0.6	0.3	0.7	0.4	0.9
LP1/LP2 slope of regression function	0.64	0.71	0.64	0.80	0.73	0.87	0.80	0.72	0.71	0.87	0.74	0.92	0.69	0.92	0.66	0.72
	0.2	0.1	0.3	0.3	0.3	0.4	0.4	0.3	0.2	0.3	0.3	0.3	0.2	0.2	0.2	0.3

Mean latency (ms) and mean landing position (degrees) of the first and the second saccades, mean second saccade amplitude (degrees) and mean slope of the relationship between the first and the second saccade landing positions for the one-object and the two-object conditions in the prosaccade and the antisaccade tasks for the Gap-0 and the Overlap-600 ms paradigms. In the one-object conditions, the object could be of 10 or 12 crosses whereas in the two-object conditions, the first object was of 5 crosses followed by a 4- or a 6-cross object. The objects could be presented to the right or to the left side from the initial fixation cross. Standard deviations are given in italics.

object. The slope between first and second saccade landing position should then be close to 1.

Fig. 2 presents the relationship between first and second saccade landing positions in the one-and two-object conditions for the two preparation times (Gap-0 and Overlap-600) and the two saccade tasks. In order to pool data from different sides (left and right) and different lengths (10 and 12 crosses), we normalized the data in the following way. For each subject, the average first and second saccade landing position obtained in each condition, resulting from the crossing of the Number of object × stimuli Length × stimuli Side was set at 0 for each session (i.e. a given saccade task and a given presentation time) and each observed landing position centered relative to this. Such normalization of the individual data allowed us to plot the relationship between first and second saccade landing positions across all subjects as represented in Fig. 2.

In the prosaccade task, for both preparation times, the results were in accordance with previous studies. When the second saccade of the sequence was directed to a new object, the slope of the function plotting second saccade landing

position against first saccade landing position was close to 0.5, demonstrating that the saccadic system took into account the first saccade landing position in order to aim for the centre of gravity of the remaining stimulation beyond it. When the second saccade of the sequence was directed within the same object, the slope was close to 1, indicating that the second saccade was coded as a fixed motor vector applied irrespective of the first saccade landing position. The pattern is clearly different in the antisaccade task in which no difference was found between one-(1OB) and two-object (2OB) conditions for both preparation times. The analysis of variance performed on the mean normalized slopes (see Table 1)² did not show significant effects of the preparation time, the object side ($F_s < 1$), the task ($F(1,6) = 1.97$ ns) or object length ($F(1,6) = 1.72$ ns). More interestingly for our purpose, the analysis of

² Note that the slopes presented in Fig. 2 and Table 1 are different. In Fig. 2, we plotted together the normalized data across all subjects for each condition and then the slopes are computed from this overall correlation. In Table 1, the slopes presented are computed as the average of each individual's normalized slope.

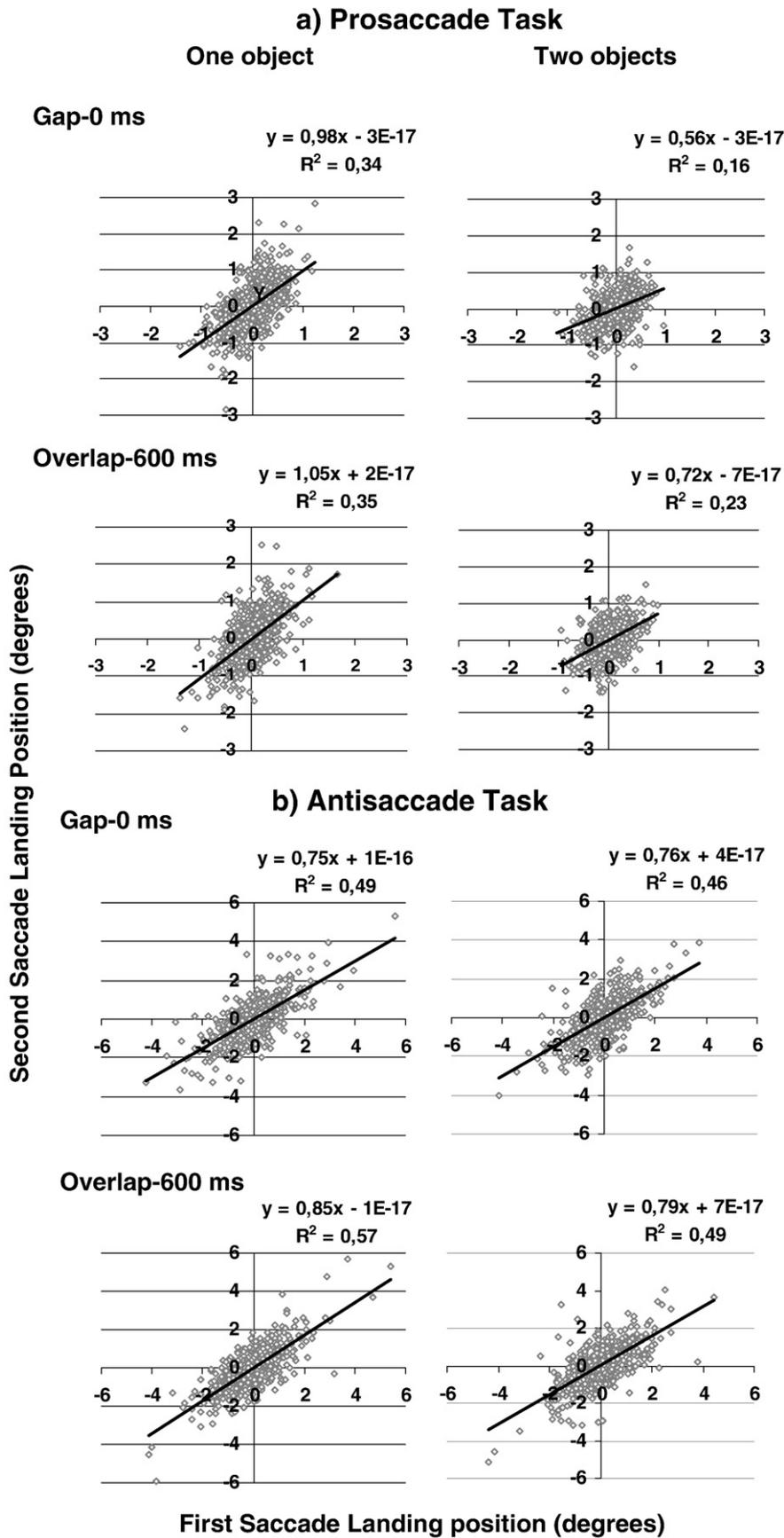


Fig. 2 – Experiment 1. Relationship between the landing position of the first and the second saccades (in degrees) for the one-object and the two-object conditions in the prosaccade and the antisaccade tasks for the Gap-0 and the Overlap-600 ms paradigms.

variance revealed an effect of the number of objects (mean slopes of 0.69 and 0.88 for 2OB and 1OB conditions respectively, $F(1,6)=12.31$, $p<.01$) that interacted with the task and the preparation time ($F(1,6)=6.20$, $p<.05$). In the prosaccade task, the mean slopes of 0.57 and 1.03 obtained for 2OB and 1OB conditions with the Gap-0 delay were significantly different ($F(1,6)=10.79$, $p<.01$), as well as the mean slopes of 0.68 and 0.99 obtained with the Overlap-600 delay ($F(1,6)=6.49$, $p<.04$). In the antisaccade task, no difference was found between 1OB and 2OB conditions for both preparation times (Gap-0: respectively 0.70 and 0.78, $F<1$; Overlap-600: respectively 0.81 and 0.75, $F<1$). We performed Student T-tests in order to determine if these mean slopes were closer to 1 or 0.5, predicted by the use of specific reference frames. In the prosaccade task, as expected for both delays, the slope obtained in the 1OB condition differed from 0.5 (Gap-0 : $t_{[5]}=4.07$, $p<.01$; Overlap-600 : $t_{[5]}=5.07$, $p<.01$) and not from 1 (Gap-0 : $t_{[5]}=0.24$ ns ; Overlap-600 : $t_{[5]}=0.08$ ns) whereas the slope obtained in the 2OB condition did not differ from 0.5 (Gap-0 : $t_{[5]}=1.05$ ns ; Overlap-600 : $t_{[5]}=2.54$ ns) but differed from 1 (Gap-0 : $t_{[5]}=6.97$, $p<.001$; Overlap-600: $t_{[5]}=5.01$, $p<.01$). Much less clear were the test results in the antisaccade task: the slope obtained in the 1OB condition differed from 0.5 (Gap-0: $t_{[5]}=3.11$, $p<.05$; Overlap-600 : $t_{[5]}=5.34$, $p<.01$) but also from 1 (Gap-0: $t_{[5]}=4.76$, $p<.01$; Overlap-600: $t_{[5]}=3.33$, $p<.05$). The slope obtained in the 2OB condition differed neither from 0.5 nor from 1 in the Gap-0 delay ($t_{[5]}=2.13$ ns and $t_{[5]}=1.67$ ns, respectively) and differed from 0.5 and from 1 in the Overlap-600 delay ($t_{[5]}=5.40$, $p<.01$ and $t_{[5]}=5.43$, $p<.01$, respectively).

2.1.2.2. Latencies. These results suggest that whereas the coding of the second saccade was clearly different between the two types of objects in the prosaccade task, the saccadic system failed to maintain the specificity of the reference frame used for the coding of the between- and within-object saccades in the antisaccade task. We expected that the absence of specific coding of between- and within-object saccade in the antisaccade task should therefore not be associated with the difference generally found on their saccade latencies, due to the supplementary updating process required when the second saccade aims for a new object. We performed an analysis of variance on the second saccade latencies (see Table 1). The effect of the number of objects was found to be significant ($F(1,6)=9.28$, $p<.02$), indicating longer between-object (329 ms) than within-object saccade latencies (295 ms). The interaction between the number of objects, the saccade task and the preparation time was not significant ($F(1,6)=2.08$ ns). The two different codings of the second saccade were associated with different second saccade latencies for the prosaccade task in both delay conditions (Gap-0 : 2OB, 320 ms vs 1OB, 283 ms, $F(1,6)=6.38$, $p<.04$; Overlap-600, 2OB, 423 ms vs 1OB, 352 ms, $F(1,6)=5.92$, $p<.05$). Although differences were also observed between the two object types, they failed to reach significance in the antisaccade task (Gap-0 : 2OB, 281 ms vs 1OB, 264 ms, $F(1,6)=3.21$ ns; Overlap-600, 2OB, 294 ms vs 1OB, 280 ms, $F(1,6)=3.58$ ns).

2.1.2.3. Saccade amplitudes. As no specific coding of the between- and within-object saccade was found in the antisaccade task, the question arises as to whether the

saccadic system is still able to maintain more basic spatial properties of the stimuli, such as their length, or if antisaccade programming is limited to the inversion of a saccade direction and not a specific amplitude. As shown in Table 1, the mean second saccade amplitude increased with the size of the stimuli (2.2° for 10-cross stimuli vs 2.5° for 12-cross stimuli, $F(1,6)=66.52$, $p<.0003$). The interaction between the stimuli length, the number of objects, the task and the preparation time was not significant ($F<1$). However, planned comparisons showed that in the prosaccade task, the second saccade amplitude became larger with the length of the stimuli for both preparation times in the two-object conditions (Gap-0: 2.3° for L5+4 vs 2.7° for L5+6, $F(1,6)=42.22$, $p<.0008$; Overlap-600: 2.3° for L5+4 vs 2.7° for L5+6, $F(1,6)=39.26$, $p<.0009$) as well as in the one-object conditions (Gap-0: 2.4° for L10 vs 2.8° for L12, $F(1,6)=55.14$, $p<.0004$; Overlap-600: 2.4° for L10 vs 2.9° for L12, $F(1,6)=33$, $p<.001$). The pattern of results was quite different in the antisaccade task as the length effect was found only in 1OB conditions for both preparation times (Gap-0: 1.9° for L10 vs 2° for L12, $F(1,6)=12.11$, $p<.01$; Overlap-600: 2.1° for L10 vs 2.4° for L12, $F(1,6)=8.86$, $p<.02$) but not in 2OB conditions (Gap-0: 1.9° for L5+4 vs 2° for L5+6, $F(1,6)=1.15$ ns; Overlap-600: 2.2° for L5+4 vs 2.4° for L5+6, $F(1,6)=2.68$ ns). None of the other main factors had a significant effect (number of objects and object side, $F_s<1$; preparation time, $F(1,6)=1.04$ ns and saccade task, $F(1,6)=2$ ns).

2.2. Discussion

In the prosaccade task, for both preparation times, we replicated results found in previous studies using other types of spatially-extended objects such as isolated words or geometrical objects (e.g. Vergilino and Beauvillain, 2001; Vergilino-Perez and Findlay, 2006). By contrasting the nature of the action to be performed by the movement –to move to a new object or to explore the current one with a second saccade, we replicated, in the prosaccade condition, that the spatial information relevant for the saccade is coded in different reference frames (see Introduction).

More interesting is the saccadic system's response when it is asked to perform a mirror exploration of the objects as required in the antisaccade task. In this case, we found that whatever the time available for encoding the peripheral stimulation – i.e. the latency of the first saccade in the Gap-0 condition and additional 600 ms in the Overlap-600 condition – the saccadic system fails to apply a reference frame specific to the visual stimulation. For both one-object and two-object conditions, the slope of the relationship between first and second saccade landing position could not be compared to the predicted values of 1 or 0.5. One could argue that this is due to the greater variability obtained on saccade landing positions in the antisaccade task. Indeed, this is a valid argument for within-object saccades as their amplitude was still influenced by the stimulus length. It is possible that the saccadic system inverted the second saccade plan but the variability of the antisaccade landing positions did not allow us to replicate the relationship between first and second saccade landing positions. However, an alternative explanation lies in the time available for the saccade planning. Whereas in the prosaccade task, all the preparation time before the execution of the initial saccade can be devoted to the planning of the two-saccade

sequence, this is clearly not the case in the antisaccade task in which additional processes linked to the inhibition of the prosaccades and the programming of the antisaccade take place. We can suppose that in the one-object condition, the time available before the execution of the first antisaccade allowed the saccadic system to encode the visual representation of the object but not to complete motor programming of the saccade sequence.

For between-object saccades, the saccadic system did not seem to use a retinocentric reference frame as in the prosaccade task. Indeed, the indicators of the updating process during the fixation on the first object, i.e. the slope close to 0.5, and longer latencies than for within-object saccades, were not found in the antisaccade task. Moreover, the amplitude of the second between-object saccade did not depend on the stimuli length. One could argue that the updating process did not occur during the first fixation after the first antisaccade because no visual information about the size of the object was available at this time. However, the retinocentric reference frame involved in the coding of between-object saccades was previously observed in a prosaccade task in which the two saccades of the sequence were memory-guided, the first saccade being executed after a memorization delay of 300 ms (Beauvillain et al., 2005). In such memory-guided saccade task, the updating processes still occurred, on the basis of the second object location stored in spatial memory. In the present experiment, it is possible that the trace of the second object stored in spatial memory was lost or not strong enough to be used or perhaps even never encoded. Just like for within-object saccades, we suggest that the saccadic system does not have sufficient time before the execution of the first saccade to successfully plan the saccade sequence. Moreover, the preparation time could be insufficient to correctly encode the length of the second object.

We conducted a second experiment in which we further reduced the preparation time for the two-saccade sequence by using a Gap-200 paradigm in which the fixation point was extinguished 200 ms before target object appearance. Such a procedure should decrease the latency of the first saccade and consequently the preparation time available for the planning of the two-saccade sequence. We expect that the time reduction will suppress the length effect found for the one-object condition in the antisaccade task. The specific coding of the between- and within-object has never been examined with this paradigm and it is possible that even in the prosaccade task, the saccadic system might not have enough time to plan the two-saccade sequence based on a specific reference frame.

3. Experiment 2

In this experiment, we used a Gap-200 ms paradigm, to reduce the time interval available before the execution of the two-saccade sequence. As the increase of the gap has been shown to increase the number of erroneous prosaccades in the antisaccade task (e.g. Fischer and Weber, 1997), we have introduced two modifications relative to Experiment 1 in order to increase the number of trials. First, the distracters were suppressed and second, each subject was submitted to 6 antisaccade sessions and 2 prosaccade sessions.

3.1. Results

3.1.1. First saccade of the two-saccade sequence

3.1.1.1. Latencies. As in Experiment 1, mean first saccade latencies were significantly longer in the antisaccade task compared to the prosaccade task (respectively, 221 ms versus 165 ms, $F(1,5)=19.73$, $p<.007$, see Table 2). The effect of the number of objects, the length and the side of the stimuli were not significant (respectively, $F(1,5)=3.33$ ns; $F(1,5)=4.30$ ns; $F(1,5)=1.30$ ns). Note that as expected, the latencies obtained with the Gap-200 ms delays were shorter than those obtained in Experiment 1 with the Gap-0, and the Overlap-600 ms delays. However, only a small percentage of saccades can be considered as express saccades in this experiment (respectively, 4.1% and 0.17% of the data in the prosaccade and antisaccade trials).

3.1.1.2. Landing positions. The first saccade landing position was farther into the stimulus in the antisaccade task compared to the prosaccade task (respectively, 4.4° versus 2.9° , $F(1,5)=9.13$, $p<.03$, see Table 2). Others factors had no significant effect ($F(1,5)=1.26$ ns for the number of objects; $F(1,5)=4.63$, $p<.08$ for stimuli length and $F(1,5)=1.41$ ns for the side of the stimuli).

3.1.2. Second saccade of the two-saccade sequence

3.1.2.1. Relationship between the first and second saccade landing positions. Of interest here is the regression function between first and second saccade landing positions which reveals how the second saccade is coded. Fig. 3 presents the relationship between first and second saccade landing positions in the one-object and two-object conditions for the two saccade tasks. The data were normalized by the procedure presented in Experiment 1 (see section 2.1.2).

In the prosaccade task, the results obtained in the one-object condition are in favour of an oculocentric reference frame for the coding of the within-object saccade. The slope close to 1 indicates that the second saccade was not updated on the basis of the first saccade but coded as a fixed motor vector applied irrespective of the first saccade's landing position. In the two-object conditions, we expected a slope close to 0.5 as a sign of the updating process during the fixation on the first object on the basis of the retinal positions of the objects. However, with the Gap-200 ms procedure, we failed to replicate the use of such a retinocentric reference frame, as we found a slope close to 0.75. In the antisaccade task, the slope of the relationship is close to 1 for both object conditions, suggesting a coding of the second saccade in an oculocentric reference frame. The analysis of variance performed on the mean normalized slopes (see Table 2) showed no significant effect of the number of objects (mean slopes of 0.85 and 0.89 for 2OB and 1OB conditions respectively, $F<1$) and no interaction with saccade task ($F<1$). The effect of others factors did not reach significance on the regression slopes ($F(1,5)=3.92$ ns for the saccade task; $F<1$ for stimuli length, and $F(1,5)=3.06$ ns for the side of the stimuli). The results of the Student T-tests showed that for both saccade tasks and for both object conditions, the slopes differed from the value of 0.5 (Prosaccade: 2OB: $t_{[4]}=2.93$, $p<.05$; 1OB: $t_{[4]}=2.84$,

Table 2 – Experiment 2

	1 object (1OB)				2 objects (2OB)			
	10 crosses		12 crosses		5+4 crosses		5+6 crosses	
	Right	Left	Right	Left	Right	Left	Right	Left
<i>Prosaccades</i>								
1st sac latency (ms)	165	166	169	165	161	160	167	165
	30	15	27	14	23	12	27	14
1st sac landing position (°)	2.6	2.8	2.7	3	2.8	3.1	2.8	3.1
	0.4	0.8	0.4	0.9	0.4	0.6	0.4	0.60
2nd sac latency (ms)	348	323	331	312	326	364	312	334
	108	121	99	133	82	189	71	145
2nd sac landing position (°)	5.7	5.2	6.3	5.8	5.4	5.2	5.8	5.6
	0.5	0.2	0.8	0.3	0.5	0.1	0.8	0.2
2nd sac amplitude (°)	3	2.4	3.7	2.9	2.6	2.2	3	2.5
	0.8	0.7	1.1	0.9	0.8	0.5	1	0.7
LP1/LP2 slope of regression function	0.70	0.99	0.78	0.89	0.81	0.85	0.85	0.57
	0.31	0.53	0.31	0.45	0.25	0.33	0.57	0.33
<i>Antisaccades</i>								
1st sac latency (ms)	224	219	224	219	223	219	223	216
	28	26	27	24	28	28	28	26
1st sac landing position (°)	4.4	4.3	4.4	4.4	4.3	4.4	4.4	4.4
	1.6	1.4	1.6	1.3	1.7	1.3	1.7	1.4
2nd sac latency (ms)	206	208	197	194	237	227	222	217
	78	101	86	90	132	132	112	123
2nd sac landing position (°)	6.9	7.5	7	7.9	6.8	7.6	6.9	7.8
	1.9	2.2	1.8	2.1	1.9	2.3	2	2.2
2nd sac amplitude (°)	2.5	3.3	2.6	3.5	2.5	3.2	2.5	3.4
	0.7	1.1	0.7	1	0.7	1.2	0.7	1.1
LP1/LP2 slope of regression function	0.88	1.02	0.87	1.03	0.86	0.95	0.91	1.00
	0.16	0.17	0.06	0.14	0.24	0.15	0.25	0.16

Mean latency (ms) and mean landing position (degrees) of the first and the second saccades, mean second saccade amplitude (degrees) and mean slope of the relationship between the first and the second saccade landing positions for the one-object and the two-object conditions in the prosaccade and the antisaccade tasks. In the one-object conditions, the object could be of 10 or 12 crosses whereas in the two-object conditions, the first object was of 5 crosses followed by a 4- or a 6-cross object. The objects could be presented to the right or to the left side from the initial fixation cross. Standard deviations are given in italics.

$p < .05$; Antisaccade: 2OB: $t_{[4]} = 5.69$, $p < .01$; 1OB: $t_{[4]} = 10.90$, $p < .001$) and the slopes did not differ from the value of 1 (Prosaccade : 2OB: $t_{[4]} = 2.34$ ns; 1OB: $t_{[4]} = 1.38$ ns; Antisaccade : 2OB: $t_{[4]} = 0.91$ ns; 1OB: $t_{[4]} = 1.24$ ns).

3.1.2.2. Latencies. We expected no second saccade latency difference between the 1OB and 2OB conditions as no updating processes occurred during the fixation on the first object in the latter condition (see above). The analysis of variance performed on the mean second saccade latencies (see Table 2) showed no significant effect of the number of object (2OB: 280 ms vs 1OB: 265 ms, $F(1,5) = 2.53$ ns) and no interaction with the task ($F(1,5) = 1.29$ ns). The analysis of variance also revealed an effect of the task, second prosaccade latencies being longer than second antisaccade latencies (331 ms vs 214 ms, $F(1,5) = 7.84$, $p < .03$), and no significant effects of others factors ($F(1,5) = 4.58$, $p < .8$ for stimuli length and $F < 1$ for the side of the stimuli).

3.1.2.3. Saccade amplitudes. Regression slopes and second saccade latencies observed in the Gap-200 procedure suggest that an oculocentric reference frame was used for the planning of the second saccade whatever the object condition

and saccade task. However, such an interpretation would be supported only if the second saccade amplitude still presented the length effect, signalling a correct encoding of the peripheral visual stimulation. Indeed, a slope close to 1 between first and second saccade landing positions can also simply mean the application of a second stereotyped saccade. In other words, the decision to make two saccades is maintained without the specific metrics relative to the spatial information relevant for the planning of the second saccade. As shown in Table 2, the mean second saccade amplitude increased with the stimuli length (2.7° for 10-cross stimuli vs 3° for 12-cross stimuli, $F(1,5) = 32.6$, $p < .003$). The interaction between the stimuli length, the number of objects and the saccade task was significant ($F(1,5) = 13.85$, $p < .01$). In the prosaccade task, the second saccade amplitude became larger with the stimuli length for 1OB (L10: 2.7° vs L12: 3.3° , $F(1,5) = 36.92$, $p < .002$) as well as for 2OB (L5+4: 2.4° vs L5+6: 2.8° , $F(1,5) = 20.72$, $p < .006$). This was not the case in the antisaccade task in which the length effect was found neither for 1OB (L10: 2.9° vs L12: 3° , $F(1,5) = 2.47$ ns) nor for 2OB (L5+4: 2.9° vs L5+6: 3° , $F(1,5) = 2.81$ ns). Note that none of the other factors showed a significant effect (saccade task and side of the stimuli, $F_s < 1$ and number of objects, $F(1,5) = 1.5$ ns).

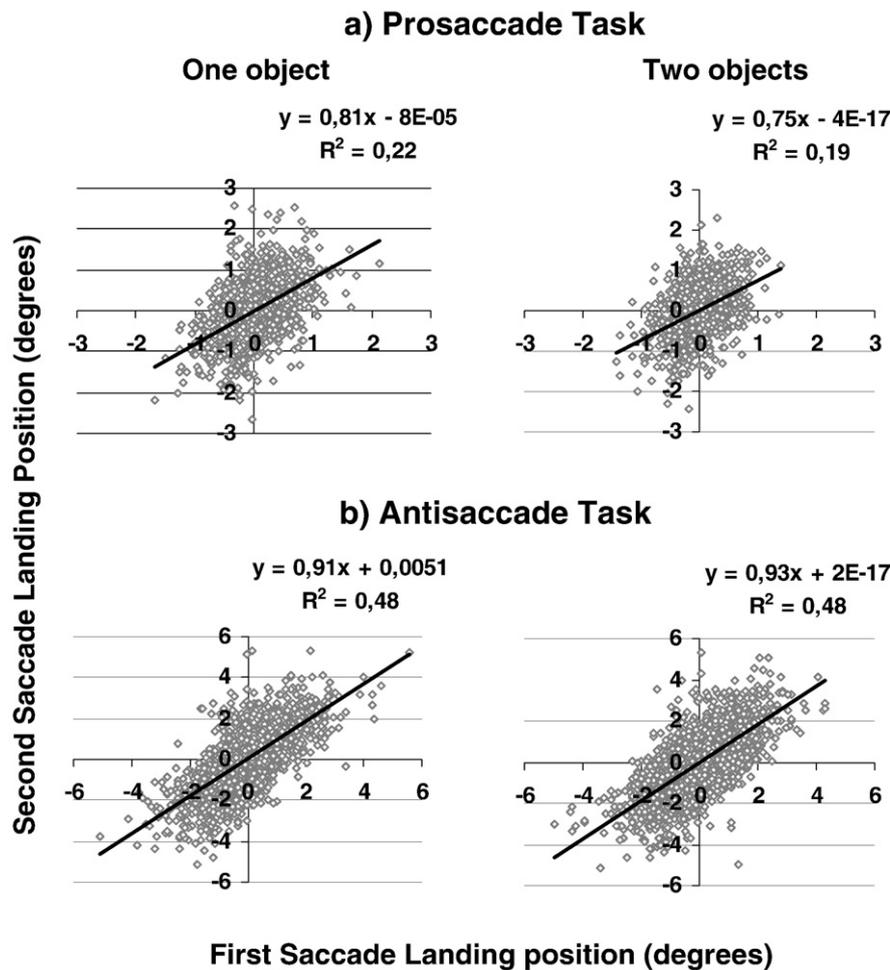


Fig. 3 – Experiment 2. Relationship between the landing position of the first and the second saccades (in degrees) for the one-object and the two-object conditions in the prosaccade and the antisaccade tasks for the Gap-200 ms paradigm.

3.2. Discussion

The use of a Gap-200 paradigm prevented the saccadic system from using a retinocentric reference frame to code a sequence of two saccades. This was true for both pro- and antisaccades. Whatever the object structuration, the second saccade is calculated as a fixed motor vector which is not updated after the first saccade. For prosaccades, this vector is based on second object size, but for antisaccades, object size is not yet taken into account, as if only the decision to make a second saccade had been retained, but not its metrics.

4. Influence of time on the reference frame and updating processes

Taken together, the two experiments presented here indicate that the time available before first saccade onset is essential for determining how an upcoming saccadic sequence is planned. Indeed, the shorter first saccade latencies generated by the Gap-200 ms paradigm were sufficient to alter the reference frame specificity. If timing is crucial for the

application of a specific reference frame, we should be able to measure it more finely by looking at the influence of first saccade latency on reference frame. One could expect that the application of a specific reference frame was more effective for longer first saccade latencies compared to shorter ones, in particular in the prosaccade trials. Indeed, in the antisaccade trials, the concurrent processes may impede any influence of the first saccade latency. To refine the analysis of the time necessary to plan the saccade sequence relative to the object segmentation, we performed an additional analysis in which the relationship between first and second saccade landing positions was examined for short and long first saccade latencies (defined by the median) for pro- and antisaccade tasks in the three delay conditions. We performed Student t-Tests to compare each mean normalized slope obtained to the predicted value of 1 and 0.5. The results are summarized in Table 3.

For the Gap-0 and Overlap-600 ms prosaccades trials, within-object saccades were coded as a fixed motor vector as shown by the slopes close to 1 for both short and long first saccade latencies whereas the between-object saccades were updated relative to the first saccade landing position on the

Table 3 – Mean slopes of the relationship between the first and the second saccade landing positions for the one-object and the two-object conditions in the prosaccade and the antisaccade tasks for the Gap-0 and the Overlap-600 (Experiment 1) and the Gap-200 (Experiment 2) paradigms

	Gap-0 ms		Overlap-600 ms		Gap-200 ms	
	1OB	2OB	1OB	2OB	1OB	2OB
<i>Prosaccades</i>						
1st sac latency (median)	174 ms	171 ms	192 ms	188 ms	158 ms	157 ms
Short	1.03 **	0.60 ⁺⁺	0.93 *	0.69 ⁺⁺	0.78	0.80 *
	<i>.29</i>	<i>.19</i>	<i>.29</i>	<i>.20</i>	<i>.31</i>	<i>.22</i>
Long	0.76 *	0.55 ⁺⁺	1.09 **	0.67 ⁺⁺	0.97	0.66
	<i>.26</i>	<i>.13</i>	<i>.28</i>	<i>.20</i>	<i>.46</i>	<i>.31</i>
2nd sac latency (median)	268 ms	281 ms	328 ms	385 ms	304 ms	293 ms
Short	1.10 *	0.62 ⁺⁺	1.09 *	0.53 ⁺⁺	0.73	0.62
	<i>.47</i>	<i>.21</i>	<i>.44</i>	<i>.28</i>	<i>.63</i>	<i>.44</i>
Long	1.20 *	0.53 ⁺⁺	0.93 ***	0.78 ⁺⁺	0.64	0.79
	<i>.56</i>	<i>.15</i>	<i>.14</i>	<i>.15</i>	<i>.47</i>	<i>.32</i>
<i>Antisaccades</i>						
1st sac latency (median)	259 ms	263 ms	225 ms	218 ms	219 ms	217 ms
Short	0.67 ⁺⁺⁺	0.84 ⁺⁺⁺	0.84 **	0.80 ⁺⁺⁺	0.95 **	0.95 **
	<i>.12</i>	<i>.15</i>	<i>.20</i>	<i>.12</i>	<i>.24</i>	<i>.19</i>
Long	0.68*	0.59	0.75 ^{**}	0.73 ^{**}	0.90 ***	0.90 *
	<i>.32</i>	<i>.43</i>	<i>.18</i>	<i>.18</i>	<i>.10</i>	<i>.23</i>
2nd sac latency (median)	250 ms	263 ms	286 ms	293 ms	166 ms	175 ms
Short	0.73 ⁺	0.75	0.72 ⁺⁺	0.75 ⁺⁺	0.97 **	1.08 *
	<i>.23</i>	<i>.48</i>	<i>.16</i>	<i>.17</i>	<i>.17</i>	<i>.46</i>
Long	0.77 ⁺⁺⁺	0.77	0.84 ⁺⁺⁺	0.71 ⁺⁺⁺	0.96 ***	0.91 **
	<i>.12</i>	<i>.37</i>	<i>.16</i>	<i>.17</i>	<i>.11</i>	<i>.20</i>

The data are divided relative to the median of the first and second saccade latencies (ms). Standard deviations are given in italics. The presence of symbols + and * indicates slopes different from the predicted values of 1 and 0.5 respectively. One, two or three symbols indicate Student T-tests $P < .05$, $P < .01$ and $< .001$ respectively. Remember that each slope is compared to the predicted values of 0.5 and 1.

first object to aim for a spatial position on the second object as indicated by the slopes close to 0.5. The t-tests corroborate the fact that the within-object saccades did not differ from the predicted value of 1 but differed from 0.5 whereas the between-object saccades did not differ from the predicted value of 0.5 but differed from 1. The results were less consistent for prosaccade task in the Gap-200 delay. The slopes were close to 1 for the one-object condition even if the comparisons between the predicted value of 0.5 and the slopes of 0.78 and 0.97 obtained for short and long first saccade latencies respectively were only marginal ($t_{[4]} = 2.24$, $p < .09$, $t_{[4]} = 2.48$, $p < .07$). More interestingly, an influence of timing on the reference frame emerges in the 2OB condition. Indeed, the slope close to 1 obtained for short first saccade latencies suggests a coding of the second saccade as a fixed motor vector. The T-tests indicate a significant difference from the predicted value of 0.5 ($t_{[4]} = 3.34$, $p < .05$) and only a marginal difference from the predicted value of 1 ($t_{[4]} = -2.21$, $p < .10$). So, as obtained for the mean analyses presented in the results of Experiment 2, the planning of the second between-object saccade seems to be impaired when insufficient time is given to the system before first saccade execution. For longer first saccade latencies, the slope of 0.66 gets closer to the predicted value of 0.5 as shown by the T-test very close to the significant threshold ($t_{[4]} = -2.64$, $p < .057$). So, even if the effects were only marginal, such an analysis suggests that the saccade sequence directed to two objects could be coded in a retinocentric reference frame with the Gap-200 ms delay.

We also examined the relationship between first and second saccade landing positions when the data were divided relative to median second saccade latency for both object and delay conditions in the prosaccade and antisaccade tasks. First, we examined the possible use of a consistent reference frame that might appear only for longer second saccade latencies in the antisaccade task. However, the main goal of this analysis was to check if the fixed motor vector found for within-object prosaccades in the three delays as well as for between-object prosaccades in the Gap-200 ms delay could be updated during the first fixation if enough time is available.

Indeed, one could argue that the coding of the saccade as a fixed motor vector was due to a lack of time available to update the motor plan relative to the visual information available after the first saccade. In other words, such a fixed-vector planning could be seen only for short second saccade latencies whereas the updating processes could occur with longer ones. This hypothesis is based on the fact that the latency of saccades coded as fixed-motor vector is shorter than the latency of the updated saccades. However, as previously found by Vergilino-Perez and Findlay (2006) that examined this question in a visual search task, the analysis presented in Table 3 also did not reveal any effect of second saccade latency on the relationship between first and second saccade landing position for pro and antisaccade tasks in the three delays. This suggests that once the reference frame has been selected relative to the peripheral visual information, it is not modified after the first saccade of the sequence, whatever the time available.

5. General discussion

In two experiments, we used different experimental procedures to investigate the importance of the time interval necessary for the saccadic system to plan a sequence of saccades. First, we manipulated the duration of the preparation time before first saccade onset by contrasting different paradigms that modulate first saccade latency. By giving the signal for the first saccade execution before, at the same time or after the stimuli presentation, we let the saccadic system have more or less time to integrate the peripheral stimulation and to plan the saccade sequence. Second, we contrasted two different saccadic tasks, a prosaccade task in which subjects had to explore the visual objects and an antisaccade task in which they had to do the same exploration but in the opposite direction. The antisaccade is a more time-consuming task because the system has not only to remember the visual representation of the structure of stimuli and to invert the saccade plan but also to inhibit the sequence of prosaccades (at least the first one).

5.1. The planning of two-saccade sequences is time-dependent

In Experiment 1, using Gap-0 ms and Overlap-600 ms paradigms, we replicated the results found in previous studies using different kinds of stimuli – isolated words, non-sense letter strings, geometrical objects – and different saccadic tasks – visually or memory-guided saccades (e.g. Vergilino and Beauvillain, 2001; Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006). We showed here that the sensorimotor transformation process implements different coding depending on the action to be performed – to move to a new object or to explore the current one with a second saccade. When the second saccade of the sequence aims for a new object, the saccade is updated after the first saccade in a retinocentric reference frame with respect to the new eye position, in order to aim for the center of gravity of the new object. Alternatively, when the second saccade explores the same object, the saccade does not aim for a specific target location but rather is coded in an oculocentric reference frame as a fixed motor vector applied irrespective of the initial landing position on the object. The use of different reference frames would involve the use of different object properties. Whereas between-object saccades are computed relative to object location, within-object saccades are calculated based on object size. Moreover, this implies a difference in the way second saccades are planned before the execution of the first saccade. Indeed, the fact that the within-object is not updated after the first saccade as a function of the eye position indicates that the saccade is preplanned before the first saccade on the basis of the object size (Vergilino and Beauvillain, 2000). The two saccades of the sequence can be seen as an entire unit planned before the first saccade and executed as a whole (Ditterich et al., 1998; Inhoff, 1986; Zingale and Kowler, 1987), and the oculocentric representation should be supported by a non-visual motor memory maintaining the future movement to be executed (Fuster, 1996). For between-object saccades, the motor vector of the saccade seems to be computed after the

first saccade relative to the new eye position to aim for a spatial location on the second object. The saccadic system has to maintain the spatial location of the second object in a spatial memory before the first saccade and then update it after its execution. Therefore, from Experiment 1 we can conclude that the latency of the first saccade in the Gap-0 paradigm is sufficient for the saccadic system to encode the peripheral visual stimulation, supposing both the segmentation of the visual structuration into one or several objects and the integration of object size. The saccade sequence can then be planned with the appropriate specific reference frame.

Experiment 2 used a Gap-200 ms paradigm, known to decrease the latency of the initial saccade and consequently, the preparation time for the two-saccade sequence. Here, we found coding of both within-object and between-object saccades in an oculocentric reference frame. The second saccade was coded as a fixed motor vector depending on the object size. Recall that the only difference between the two experimental procedures was the delay available for visual stimulus encoding and sequence planning. This suggests that the saccadic system did not have enough time to correctly encode the stimulation. In other words, only a coarse encoding was possible, failing to segment the two objects and consequently the second saccade was planned in an oculocentric reference frame. Note however, that the analysis of the relationship between first and second saccade landing positions for longer first saccade latencies suggests that even with the Gap-200 ms delay, a coding of the between-object saccade in a retinocentric reference frame is possible if the visual information is presented at least 160 ms before the execution of the saccade sequence. However, it was surprising that the oculocentric reference frame was not updated during the first fixation on the first object. Indeed, Vergilino-Perez and Beauvillain (2004) showed that the initial motor plan of the within-object saccade may be subject to cancellation during the first fixation on the object. By using a paradigm in which they changed an 11-letter string in two 5-letters strings at different delays during the initial fixation on the object, they demonstrated that about 220 ms were necessary to cancel a within-object saccade and to plan a between-object saccade during the initial fixation on the object. In Experiment 2, as the latency of the second between-object was about 334 ms in the prosaccade task, we could have expected such a modification of the initial motor plan. However, we propose that the saccadic system did not update the reference frame during the fixation on the first object for two reasons. First, unlike Vergilino-Perez and Beauvillain (2004), we did not introduce here any salient modification during the initial fixation on the object that could induce the saccadic system to update the reference frame. Second, the application of the preplanned motor vector did not create an important error as the second saccade still landed in the second object, just to the right of its center. It is well known that in a double step situation, the corrective saccades occur only for initial errors greater than 2–3° (Becker and Jürgens, 1979).

Therefore, the results obtained with the Gap-200 ms paradigm suggest that the decision to plan the second saccade in a specific reference frame is taken before the execution of the first saccade of the sequence relative to the encoding of the visual peripheral stimulation. This first encoding stage

appears to be crucial, notably the segregation stage in which the object segmentation processes occur. Once selected, the reference frame does not seem to be modified during saccade sequence execution.

5.2. The two-saccade sequence planning with concurrent processes

In the antisaccade task, we examined whether the inhibition of the prosaccades and the vector inversion interfered with the preparation of the two-antisaccade sequence. Then, in addition to the manipulation of the first saccade latency, the saccadic system should benefit from more or less time to correctly plan the antisaccade sequence because of these concurrent processes. From this view, the Gap-200 ms condition could represent an extreme situation. In this case, the short first saccade latencies did not allow the saccadic system to correctly encode the visual stimulation presented in periphery and the two antisaccades were found to be stereotyped. This suggests the saccadic system has enough time to perform two antisaccades but not to plan the second saccade relative to the segmentation of the visual stimulation into one or two objects or to the stimulus size. In the Gap-0 and the Overlap-600 ms paradigms, the saccadic system benefits from more time, and a difference between the one-object and the two-object conditions was revealed. Indeed, within-object saccades are still coded on the basis of the object size even if we did not find a slope of 1 between first and second saccade landing positions in the one-object condition. We suggest that the time available before the execution of the first antisaccade allowed the saccadic system to encode the size of visual stimulation, but not the computation of the saccade metric relative to the visual information.

Interestingly, the effect of object size was not found on the second between-object antisaccade. Again, the saccadic system may not have had enough time to correctly encode the two objects. However, this result also sheds new light on what happens during the planning of the two prosaccade sequence directed to two objects. Indeed, the absence of an object size effect on the between-object antisaccade can also be explained by the fact that with between-object prosaccades, the system relies on the updating of the spatial representation of the second object occurring after the first saccade. Then, before the execution of the first saccade, the system gives more weight to the encoding of first object size relative to the second object size. The quality of encoding would depend on object eccentricity and so after the execution of the first antisaccade, the spatial representation of the second object is not accurate enough. The updating of the between-object was previously found in a memory-guided saccade task in which the saccadic system did not benefit from the visual stimulation during the fixation on the preceding object (Beauvillain et al., 2005), just like in the antisaccade task reported here. However, recall that in the antisaccade task, the system has to maintain the representation of the object in memory but also to invert it. It is possible that the additional process of vector inversion damages the visual representation.

Therefore, planning a saccade sequence is impaired by the instruction to perform antisaccades. The additional processes

of inhibition and inversion occurring during such a task seem to interfere with the planning of the sequence of saccades before the execution of the first movement. Another view is to consider that subjects did plan the sequence of saccades in a specific reference frame, but that this plan was changed after completion of the first movement. Thus, no difference would be expected as for the coding of between-object and within-object saccades. This is not the case here as an effect of object length was found on within-object saccades but not on between-object saccades. Further studies need to be conducted to examine whether this is due to a difference in the encoding of the peripheral stimulation before the execution of the first saccade or to a difference in the preservation of the motor plan in motor and spatial memories.

6. Conclusion

This study sheds new light on the role of the time available for the saccadic system to plan a sequence of saccades in a reference frame specific to the parafoveal visual structure. We showed here that in normal conditions, the latency of the first saccade of the sequence seems sufficient for the saccadic system to successfully plan a sequence in a specific reference frame. Several stages would occur in the sensori-motor transformation process: the segmentation of the visual stimulation into a single or several objects, the encoding of their respective size and the selection of a reference frame. However, the experiments presented here demonstrate that if less time is given to the saccadic system or if other processes are concurrent, then the planning of the two saccade sequence is disrupted at one of these stages. Therefore, this study provides new evidence about how the saccadic system explores visual space and reveals how visual segmentation processes affect saccade control. In particular, the time available for the integration of peripheral visual stimulation appears to be crucial for visual encoding but also for the decision to plan the two-saccade sequence in a specific reference frame, a decision that is taken before the execution of the sequence.

The coexistence of two modes of saccade planning raises the question of their respective status. One can speculate that the saccadic system uses one mode rather than the other depending on the task demands. The updating of saccadic motor plans might be more frequent for difficult tasks requiring saccadic accuracy, as for example visual search in a complex environment or reading a difficult text whereas the preplanning of the saccade might be associated to easier or more automated tasks. In other words, the dominance of one mode rather than the other could be modulated relative to the task difficulty. Extended research has to be conducted to determine the role of the task demands on saccadic planning.

7. Experimental procedures

7.1. Subjects

In each experiment, subjects with normal or corrected to normal vision participated. Some were familiar with the eye movement recording, the other were trained before the

beginning of the experiment. All gave their informed consent. Seven subjects took part in the first experiment (2 authors and 5 naive subjects) and six (1 author and 5 naive) in the second. Three subjects participated in the two experiments.

7.2. Instruments and eye movement recording

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 submaxillary dental print and forehead rest. The stimuli were presented on an Iiyama HM240DT monitor with a refresh rate of 170 Hz and a resolution of 600×800 pixels. Eye movements were monitored by a Bouis oculomotor system (Bach et al., 1983), with an absolute resolution of 6 arc minutes 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 oculometer was sampled every 2 ms. Saccades were detected with an in-house program using Labview 7.1 by velocity (>40°/s), acceleration (>3000°/s/s) and minimal displacement (0.15°) thresholds.

7.3. Materials

In the first experiment, eight types of stimuli were used, four experimental stimuli and four distracters. The experimental stimuli consisted of a series of ten or twelve 0.36°×0.41° white crosses displayed on a medium grey background. As shown in Fig. 1, the series of crosses constituted either a single long group of 10 or 12 crosses, called the one-object condition (1OB) or two separate groups, called the two-object condition (2OB). In the 2OB conditions, the first object was always constituted of 5 crosses followed by a second group of 4 or 6 crosses. In half of the trials, distracters were presented in order to avoid the learning of a stereotyped sequence of two saccades. They were constituted of two white crosses, the eccentricity between the initial fixation cross and the first cross as well as the eccentricity between the two crosses varied (see Fig. 1). In the second experiment, only the four experimental stimuli were used.

7.4. Procedure

Each session began with a full calibration procedure during which subjects had to saccade to 5 bars presented successively from left to right in steps of 3°. Reference measures were taken for each of the 5 bars. If the variability of each measure was below a threshold (0.4 V), and if they were linear, the calibration was considered successful and the experiment started. Each experimental trial started with a calibration check. A bar appeared in the center of the screen and subjects had to fixate it. If the recorded value was different from full calibration ($\pm 0.1^\circ$), the calibration was automatically renewed. When successful fixation was detected, the initial fixation cross, subtending 0.36°×0.41° of visual angle was presented at the center of the screen, indicating the beginning of the trial.

In the first experiment, one subject performed 8 sessions of 240 trials, two sessions for each experimental condition resulting from the crossing of the saccade Task (Pro-saccade vs Anti-saccade)×the Preparation time (Gap-0 ms vs Overlap-

600 ms). The saccade Task and the Preparation time were blocked for one session. In each session, the four types of experimental stimuli (2 Lengths×2 Number of objects) and the four types of distracters were presented at the left and the right of the central fixation cross, 15 times each, in a random order. In the pro-saccade sessions, the subject had to fixate the initial fixation cross and then to explore the stimuli displayed 2° to the left or to the right when the cross disappeared. The initial fixation cross disappeared simultaneously (Gap-0 ms delay) or 600 ms after the stimuli appeared (Overlap-600 ms delay). In the anti-saccade sessions, the subjects initiate a response to the mirror symmetric location to the target stimulus. We never explicitly instructed the subjects to do a two-saccade sequence. The subjects had to press a button at the end of the trial to trigger the next trial. The saccade Task and the Preparation time sessions were presented in a random order across the subjects.

In the second experiment, we suppressed the distracter trials to keep only the experimental trials and increased the number of the antisaccade sessions. Then, each subject performed 2 sessions of the prosaccade task and 6 sessions of the antisaccade task. In each session, the four type of experimental stimuli were presented 30 times each (2 Lengths×2 Number of objects×2 Sides) in a random order. The procedure was identical to the one of the first experiment except that the initial fixation cross disappeared 200 ms before the stimuli appeared.

7.5. Data analyses

In Experiment 1, we eliminated the following trials from further analyses: trials in which blinks occurred (0.9%), trials with errors in the initial saccade direction (mean 1.8% : 0.03% in Pro-Gap; 6.13% in Anti-Gap, 0.14% in Pro-Overlap and 0.86% in Anti-Overlap), trials with short (<80 ms) or long (>800 ms) initial saccade latencies (8.6%), trials in which only one saccade occurred (3.1%), trials in which the second saccade was a regression (0.5%), trials with short (<50 ms) or long (>800 ms) second saccade latencies (6.3%). Finally, in the two-object conditions, we eliminated the trials in the pro-saccade session in which the second saccade was a within-object saccade in the first or in the second object (1.8%). This criteria was not applied for the antisaccade session, due to the lack of precision of these types of saccades. The analyses were run on the remaining 77% of trials in which the two saccades of the sequence were progressive (i.e. executed in the same direction) and appropriate to the required task (i.e. directed to the stimuli in the prosaccade session and in the opposite direction in the antisaccade session). Only the experimental trials were included in the analyses. We ran a 2 (Saccade Task : Prosaccade vs Antisaccade)×2 (Preparation time : Gap-0 or Overlap-600)×2 (Number of Object : 1OB vs 2OB)×2 (Length of the stimuli : 10 vs 12 crosses)×2 (Stimuli Side : Left or Right) ANOVA.

In the second experiment, the following trials were excluded from the analyses: blinks (1.1%), errors in the initial saccade direction (9.5%), trials with short (<80 ms) or long (>800 ms) initial saccade latencies (0.6%), trials in which only one saccade occurred (1.2%), trials in which the second saccade was a regression (0.5%) or a refixation on the first or

the second object in prosaccade task (2.6%), trials with short (<50 ms) or long (>800 ms) second saccade latencies (2.5%). The analyses were run on the remaining 82% of the data that were progressive two-saccade sequence on which a 2 (Saccade Task : Prosaccade vs Antisaccade) × 2 (Number of Object : 1OB vs 2OB) × 2 (Length of the stimuli : 10 vs 12 crosses) × 2 (Stimuli Side : Left or Right) ANOVA was performed. Note that because of the percentage of trials removed from the analysis for both experiments, and the unequal number of prosaccade and antisaccade sessions in Experiment 2, the analyses of variance were performed on the means weighted by the number of trials obtained in each experimental condition of each session.

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