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Research Report

Oculomotor plasticity: Are mechanisms of adaptation for reactive and voluntary saccades separate?

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ABSTRACT

Saccadic eye movements are permanently controlled and their accuracy maintained by adaptive mechanisms that compensate for physiological or pathological perturbations. In contrast to the adaptation of reactive saccades (RS) which are automatically triggered by the sudden appearance of a single target, little is known about the adaptation of voluntary saccades which allow us to intentionally scan our environment in nearly all our daily activities. In this study, we addressed this issue in human subjects by determining the properties of adaptation of scanning voluntary saccades (SVS) and comparing these features to those of RS. We also tested the reciprocal transfers of adaptation between the two saccade types. Our results revealed that SVS and RS adaptations disclosed similar adaptation fields, time course and recovery levels, with only a slightly lower after-effect for SVS. Moreover, RS and SVS main sequences both remained unaffected after adaptation. Finally and quite unexpectedly, the pattern of adaptation transfers was asymmetrical, with a much stronger transfer from SVS to RS (79%) than in the reverse direction (22%). These data demonstrate that adaptations of RS and SVS share several behavioural properties but at the same time rely on partially distinct processes. Based on these findings, it is proposed that adaptations of RS and SVS may involve a neural network including both a common site and two separate sites specifically recruited for each saccade type.

1. Introduction

Saccadic eye movements are rapid and accurate shifts of the eyes which are permanently called for in our everyday life to gather visual information from our environment. Two main types of saccades can be distinguished (Tusa et al., 1986): voluntary (or intentional) saccades (VS) and reactive saccades (RS). VS are internally triggered toward permanent visual

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targets whereas RS are externally triggered by the sudden appearance of a novel visual target. The generation of these two types of saccades relies on two partially separate pathways, involving the frontal cortex and the occipito-parietal cortex for VS and RS, respectively (for reviews Pierrot-Deseilligny et al., 1991, 2004; Tehovnik et al., 2000; Gaymard et al., 2003). In everyday life, we usually produce a specific type of voluntary saccades to explore complex visual scenes like a landscape or a page of reading. In this paper, we will focus on this type of intentionally generated saccades and will refer to them as scanning voluntary saccades (SVS).

Keeping an optimal performance of all these saccadic responses is critical for most of our sensory–motor and cognitive activities. It is known for nearly 30 years that adaptation mechanisms maintain saccade accuracy despite physiological or pathological perturbation of the sensory–motor saccadic system or of the relationship between this system and our environment. This saccadic adaptation phenomenon has been clearly revealed in patients and in monkeys with weakened extraocular muscles (Kommerell et al., 1976; Abel et al., 1978; Optican and Robinson, 1980). It can also be experimentally induced in healthy subjects by using the non-invasive double-step target paradigm first reported by McLaughlin (1967). This protocol consists of displacing a visual target to elicit a visually triggered saccade and then, during this primary saccade, of displacing the target again to yield a post-saccadic error. Repeated iterations of these double-step trials lead adaptive mechanisms to progressively adjust the saccade amplitude and to decrease the post-saccadic error. Using this protocol, the large majority of studies have so far focussed on the adaptation of RS (see for review Hopp and Fuchs, 2004). First, adaptation of a single RS transfers to other saccades of different amplitude and/or direction, provided their vector terminates in a restricted region called the "adaptation field" (Frens and Van Opstal, 1994). Inside the adaptation field, the amount of transfer monotonically decreases as the vector separation between the non-trained and the adapted saccade increases (Miller et al., 1981; Deubel, 1987; Frens and Van Opstal, 1994; Albano, 1996; Straube et al., 1997; Noto et al., 1999; Watanabe et al., 2000). These adaptation fields suggest that the neural locus (loci) where oculomotor commands are modified during RS adaptation encode(s) the saccadic vector (eye displacement signal), rather than the saccade goal (eye position signal). Second, the adaptation of RS involves the medio-posterior part of the cerebellum (vermis and fastigial nuclei), as revealed by imaging (Desmurget et al., 1998) and clinical studies (Straube et al., 2001) in man, and by lesion studies in monkey (Optican and Robinson, 1980; Goldberg et al., 1993; Takagi et al., 1998; Barash et al., 1999). Note however that it cannot be excluded that at least part of RS adaptation occurs upstream from the cerebellum, as suggested by a recent unit activity recording study in the nucleus reticularis tegmenti pontis (NRTP) in monkeys (Takeichi et al., 2005). In addition to the cerebellum, converging evidence suggests that the main site of adaptation-related modification of motor commands lies in the brainstem, possibly at the level of – or downstream from – the superior colliculus (Kröller et al., 1996, 1999; Melis and Van Gisbergen, 1996; Frens and Van Opstal, 1997; Deubel, 1999; Edelman and Goldberg, 2002; Hopp and Fuchs, 2002; Alahyane et al., 2004). This site was further clarified by our previous study (Alahyane and Pélisson, 2005) which demonstrated that the large adaptive modification of RS amplitude was not accompanied by any change in the main sequence relationship (peak velocity versus amplitude). This finding suggested that the plastic neuronal modifications which underlie the adaptation of RS do not include the brainstem saccadic pulse generator.

By comparison to this growing knowledge of RS adaptation, the neural substrate and behavioural properties of adaptation of VS remain very little known. Yet VS, particularly SVS, represent the most common type of saccades in everyday life. Moreover, since SVS and RS are generated by different neural circuits, it is quite possible that the neural processes of adaptation and resulting behavioural properties largely differ between these two types of saccades. Thus the knowledge of RS adaptation summarized above cannot, *a priori*, be extrapolated to SVS adaptation. It is therefore crucial to specifically investigate the mechanisms underlying adaptation of SVS. Besides, some previous studies showed no or limited transfer of adaptation between RS and VS in human, suggesting that the neural mechanisms controlling adaptation of these two types of saccades are separated (Erkelens and Hulleman, 1993; Deubel, 1995; Fujita et al., 2002; Collins and Dore-Mazars, 2006). However, cautions have to be taken since these prior works have not all dealt with the same sub-type of VS and have not always measured the adaptation after-effect that allows quantification of the true adaptation level, independently of non-specific factors. Indeed, studies of RS have shown the existence of a rapid drop of adaptation-related gain change between the end of the adaptation session and the subsequent test session (Straube et al., 1997; Scudder et al., 1998; Alahyane and Pélisson, 2005). A similar gain drop cannot *a priori*, be rejected for VS, which could have a strong impact on the computation of the transfer of VS adaptation to RS. Another behavioural study (Gaveau et al., 2005) revealed that the adaptively modified gain of RS does not recover when subjects perform VS to stationary targets during a 15-min "de-adaptation" period. These results suggest thus that VS de-adaptation and RS adaptation rely on separate mechanisms. But here again, cautions have to be taken since it is still debated whether or not de-adaptation and adaptation rely on similar mechanisms. As a final note, the neural substrate of SVS adaptation has never been explored.

The present work was thus aimed at determining the properties of SVS adaptation and at testing to what extent RS and SVS adaptations differ in healthy human subjects. We focussed on the search for adaptation fields and saccade dynamics changes in SVS adaptation. We also measured the transfer of adaptation between SVS and RS. These features are potentially quite informative about the neural substrates underlying adaptations of SVS and RS. Two main possibilities can be envisioned. First, if adaptations of SVS and RS rely on completely separated processes, we expect very low values of adaptation transfer between the two saccade types. Adaptation properties however would be either different or similar. Conversely, if adaptations of SVS and RS rely on a common process, then the adaptation properties should be very similar and the adaptation transfer high and symmetrical. Part of data has been reported in an abstract form (Pélisson et al., 2005).

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2. Results

The two saccade types (RS and SVS) were tested in two separate experiments (see Fig. 1). In each experiment, rightward and leftward saccades towards 8° eccentric targets were simultaneously adapted. In the RS experiment, the classical double-step target protocol was used to reduce the RS amplitude by systematically displacing the visual target backward during the primary saccade. In the SVS experiment, subjects performed a series of 3 horizontal SVS during the exploration of a set of 4 simultaneous and permanent visual targets (T1 to T4). During each SVS, the whole scene was displaced backward. In both RS and SVS experiments, backward intra-saccadic steps amounted to 25% of the primary target separation (8°) in the first three adaptation blocks ('a25%', 'b25%', 'c25%', 144 horizontal saccades) and 40% in the last two blocks ('d40%', 'e40%', 96 horizontal saccades). Before and after this adaptation session (240 horizontal saccades), a pre-test ('pre') and a post-test ('post'), respectively, were performed to investigate the trained saccade (±8° amplitude). Untrained horizontal saccades of the same type but of different amplitudes (±5°, ±16°, ±32°) and untrained horizontal saccades of the other type (±8° amplitude) were also examined in two separate blocks in both pre-test and post-test, for each RS and SVS condition. The order of the different blocks of trials in pre-test and post-test is indicated in Experimental procedures. A de-adaptation session (i.e., recovery of saccade amplitude) was then performed to avoid cross-over effects between the two types of adaptation (RS and SVS). This de-adaptation session was followed by a post-test ('post2') to check its efficacy.

In the following analyses, the two saccade directions were pooled. Indeed, although adaptation tended to be stronger for leftward than for rightward saccades, as reported in a previous study (Alahyane and Pélisson, 2005), the difference was not statistically significant.

2.1. *Baseline properties of saccades (pre-test)*

The pre-test properties of trained (8° target eccentricity) and untrained (5°, 16° and 32° target eccentricities) RS and SVS are summarized in Table 1. Here, we compare the baseline latency, amplitude, duration and peak velocity of the two types of trained saccades recorded in the pre-test session. We found that the latency and the amplitude differed significantly between RS and SVS (latency: 247±79 ms vs. 438±157 ms, respectively; amplitude 7.1±0.2° vs. 7.5±0.4°, respectively; one-way repeated measures ANOVAs, $n=6$, $p<0.05$). These results suggest that our protocols successfully induced two different types of saccades. However, both duration (41±4 ms vs. 42±4 ms) and peak velocity (243±19°/s vs. 249±17°/s) were similar for the two saccade types ($p=0.78$ and $p=0.11$, respectively). Our findings are consistent with previous studies reporting a better accuracy and a longer latency for voluntary saccades than for reactive saccades (e.g., Lemij and Collewijn, 1989, Deubel, 1995). Note however that our SVS latencies were longer than usually reported, which can mainly be related to the discrimination task coupled to the saccade

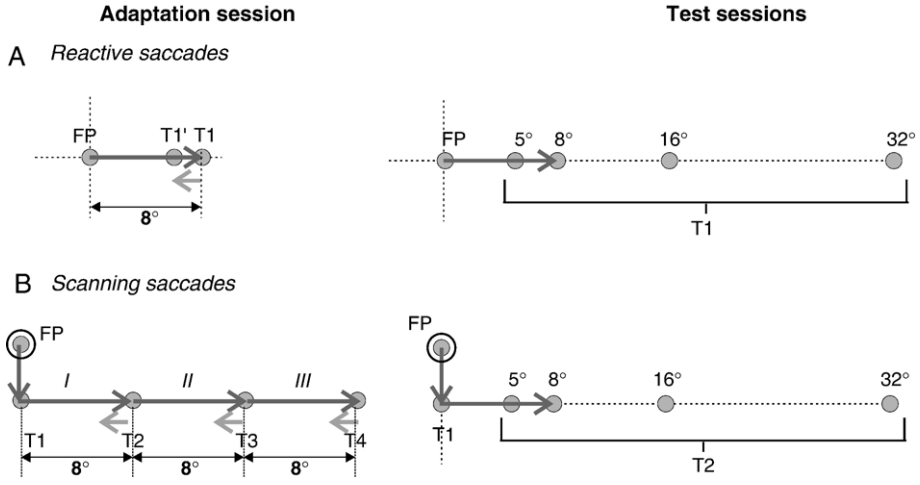

Fig. 1 – Protocols. (A) Reactive condition. The double-step target trials of the adaptation session (left panel) consisted of a first step from FP (0°) to T1 (8°) and a second backward step (small arrow) occurring during the saccade. In test sessions (right panel), single-steps from FP to T1 were presented, T1 being positioned at 4 possible locations. The peripheral target T1 was turned off during the saccade. In both adaptation and test sessions, rightward and leftward directions were tested (only the rightward direction is represented here). (B) Scanning condition. In the adaptation session (left panel), the visual scene consisted in 5 permanent visual targets including the initial fixation point (FP). Subjects successively examined these targets by performing a downward saccade from FP to T1, followed by 3 horizontal SVS. During each of these 8° horizontal saccades (I, II, III), the whole scene was displaced backward. In the test sessions (right panel), the visual scene was composed of 3 targets, eliciting first a vertical saccade from FP to T1 and second a SVS from T1 to a third target T2 which could be located at 4 possible positions. During the horizontal saccade, the whole set of targets disappeared. In both adaptation and test sessions, the rightward and the leftward directions were tested (only the rightward is illustrated here). FP: fixation point; T1: target 1; T2: target 2.

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Table 1 – Properties of reactive saccades (RS) and scanning voluntary saccades (SVS)

	Target eccentricity (deg)	Latency (ms)	Amplitude (deg)	Gain	Duration (ms)	Peak velocity (deg/s)
RS	Pre-test					
	5	208 (80)	4.5 (0.2)	0.91 (0.04)	33 (4)	179 (12)
	8	247 (79)	7.1 (0.2)	0.88 (0.02)	41 (4)	243 (19)
	16	240 (89)	13.7 (0.6)	0.85 (0.04)	58 (7)	350 (26)
	32	235 (75)	27.7 (1.2)	0.86 (0.04)	84 (7)	488 (46)
	Post-test					
	5	208 (62)	3.7 (0.3)	0.75 (0.05)	30 (5)	152 (15)
	8	216 (57)	5.7 (0.8)	0.71 (0.04)	38 (5)	221 (22)
	16	236 (90)	12.5 (0.6)	0.78 (0.04)	57 (7)	325 (34)
	32	258 (64)	26.5 (1)	0.83 (0.03)	86 (8)	458 (59)
SVS	Pre-test					
	5	412 (151)	4.7 (0.3)	0.94 (0.07)	31 (4)	183 (12)
	8	438 (157)	7.5 (0.4)	0.94 (0.05)	42 (4)	249 (17)
	16	452 (154)	14.2 (0.4)	0.89 (0.02)	61 (7)	349 (31)
	32	489 (178)	28.3 (0.9)	0.88 (0.03)	91 (16)	471 (42)
	Post-test					
	5	422 (119)	4.2 (0.3)	0.85 (0.06)	29 (5)	164 (13)
	8	493 (124)	6.4 (0.5)	0.79 (0.07)	38 (4)	219 (21)
	16	491 (138)	12.9 (0.6)	0.81 (0.04)	60 (7)	315 (42)
	32	499 (121)	27.4 (1)	0.86 (0.03)	93 (16)	446 (50)

Horizontal saccade mean (SD) latency, amplitude, gain, duration and peak velocity calculated across 6 subjects are represented for each target eccentricity, before (Pre-test) and after (Post-test) the adaptation of 8° saccades. Note that for SVS, the latency refers to the fixation duration of the starting target (see Experimental procedures).

task (Deubel and Schneider, 1996; Collins and Dore-Mazars, 2006).

2.2. *Changes in saccade amplitude: trained saccade*

2.2.1. *General features of SVS adaptation*

Fig. 2 represents raw recordings of horizontal eye movements performed by subject F during the adaptation session in the scanning condition. At the beginning of the first adaptation block ('a25%') (black trace), the 25% leftward shift of the target display during each horizontal primary saccade toward targets T2, T3′ and T4″ elicited a backward secondary saccade to reach the new target positions T2′, T3″ and T4‴, respectively. In contrast, such secondary saccades were no longer seen in the recording of the end of the third adaptation block ('c25%') (grey trace), and the primary saccades landed very close to the displaced targets.

2.2.2. *SVS adaptation versus RS adaptation*

In Fig. 3, we plotted the time course of horizontal amplitude changes for SVS (panels C, D) and RS (panels A, B). Panels A and C illustrate data from a representative subject and panels B and D depict the average data of the whole group of 6 subjects. These plots show the mean amplitude of primary saccades recorded during the following 8 successive blocks of trials: pre-test session ('pre'), 5 blocks of the adaptation session ('a' to 'e'), and the 2 post-test sessions performed immediately after the end of the last adaptation block ('post'), or after the de-adaptation session ('post2').

There was a biphasic decrease of saccade amplitude during the adaptation session, corresponding to the successive introduction of the two target perturbation sizes (25% and 40%). Also, the decrease in saccade amplitude during the last adaptation block slowed down. Note that an overshoot of about one degree of the primary saccade relative to the final target position remained uncorrected at the end of the adaptation. Most importantly, both the maximum level of saccade amplitude reduction reached during adaptation and the shape of its time course were very similar for RS and SVS.

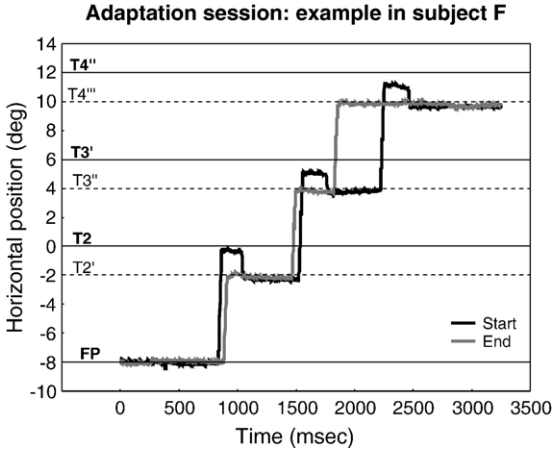

Fig. 2 – SVS adaptation session. Superimposed plots of individual trials, each containing 3 horizontal scanning saccades, are selected from the beginning of the adaptation session (black trace) and the end of the third adaptation block (grey trace) in subject F. FP: fixation point; T2, T3′ , T4″: positions of the visual targets aimed by the first, second and third horizontal primary saccades, respectively; T2′, T3″ and T4‴: corresponding positions of the same targets after a 25% backward displacement of the whole target set during each horizontal SVS.

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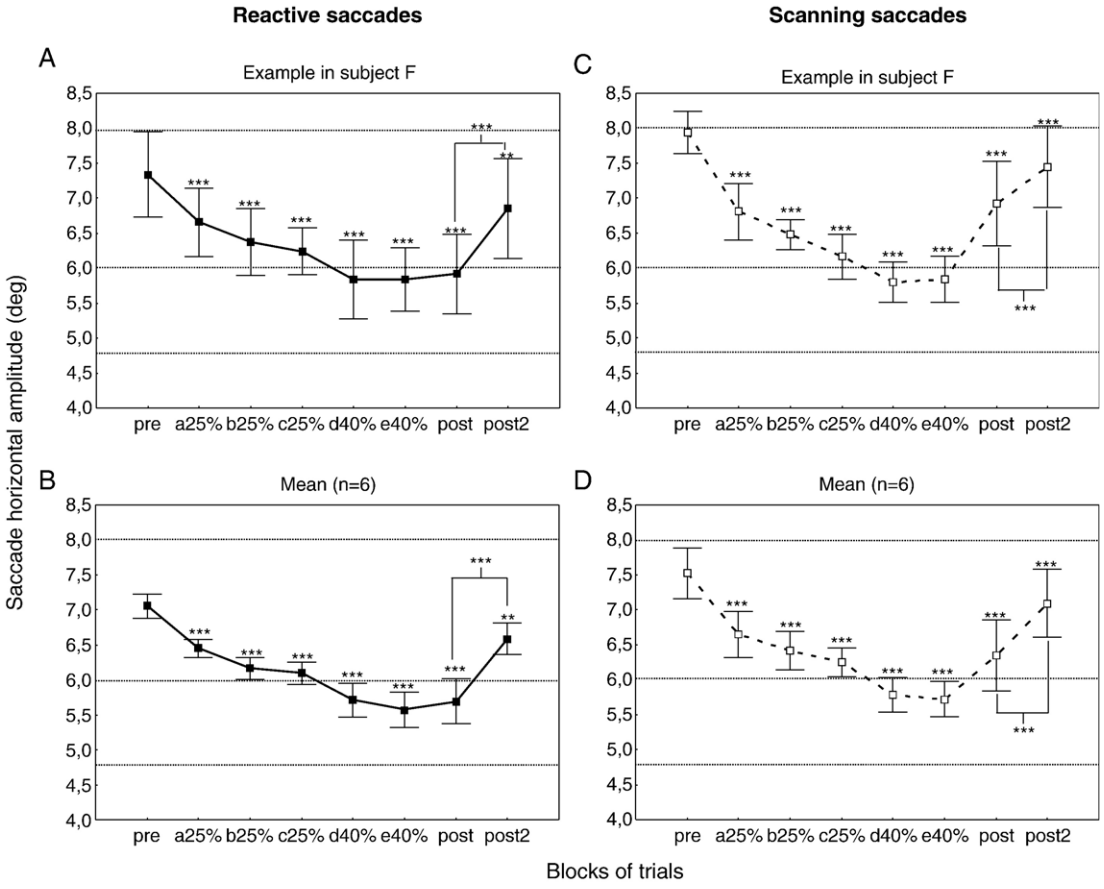

Fig. 3 – Time course of the trained saccade amplitude. Mean amplitude of reactive (panels A, B) and scanning (panels C, D) saccades is plotted as a function of blocks of trials, in subject F (panels A, C) or averaged across the 6 subjects (panels B, D). Adaptation blocks (48 saccades each) differed in the size of the intrasaccadic target step (25% of the first target eccentricity in blocks a25%, b25%, c25% and 40% in blocks d40%, e40%). Dotted lines show the primary target eccentricity (8°), the target eccentricity after a 25% step (6°) and a 40% step (4.8°). Also shown are the mean amplitudes in pre-test ('pre'), in the first post-test ('post') and in the second post-test ('post2', performed just after a de-adaptation session). Error bars are SD. Statistically significant differences of amplitude relative to pre-test or between the first and second post-tests are indicated by $^{**}p<0.01$ and $^{***}p<0.001$.

One-way repeated measures ANOVAs with « blocks of trials » as factor ($n=6$ subjects) revealed a significant main effect on saccade amplitude in both the reactive and scanning conditions ($p<0.001$) (Figs. 3B,D). More precisely, saccade amplitude was significantly reduced in the 7 last blocks as compared to the pre-test block (post-hoc LSD Fisher tests, see stars in Figs. 3B,D). RS and SVS amplitude decreased at the end of the adaptation phase relative to the pre-test by 21±2.9% and 23.9±3%, respectively (Figs. 4A,C; 'R1' and 'V1', respectively). After the adaptation session (Fig. 3, 'post'), the saccade amplitude remained significantly smaller than in the pre-test but as shown in Figs. 4A,C, the mean percent change (R2, V2) was smaller than at the end of the adaptation session (R1, V1). On average ($n=6$ subjects), we found that the after-effect (R2, V2) represented 92% and 68% of the amplitude change during adaptation phase (R1, V1) for RS and SVS, respectively (R2/R1 and V2/V1 ratios). The post-hoc analysis (LSD Fisher tests) further indicated that for RS the mean amplitude in post-test was similar to that in the two last adaptation blocks ('d40%' and 'e40%' in Fig. 3B) ($p>0.2$) whereas for SVS it was similar to that in the intermediate 'b25%' and 'c25%' blocks of adaptation ($p>0.44$). Thus either the "real" effect of adaptation, as measured by the after-effect in the post-test session, was less complete in the scanning condition than in the reactive condition, or the SVS amplitude recovered more quickly in the post-test. To differentiate between these two possibilities, we performed on each subject linear regression analyses of the amplitude versus number of saccades relationships in post-test sessions. No consistent correlation between saccade amplitude and trial number was found, both for RS ($p>0.06$) and SVS ($p>0.14$; only subject T exhibited a significant increase, $p<0.05$). Thus, these results suggest that the adaptation after-effect was smaller for SVS than for RS (Figs. 4A,C: 'R2'=−19.4±4% vs. 'V2'=−15.7±4.1%; see also 'R2' and 'V2' bars for each subject in Fig. 4B,D) although this difference did not reach statistical significance (repeated measures ANOVA ($n=6$); $F_{(1,5)}=1.92$; $p=0.22$). At last, saccade amplitude measured in the second post-test (Fig. 3, 'post2'; Figs. 4A,C, 'R3' and 'V3' bars) was substantially larger than in the first post-test (Fig. 3, 'post'), indicating a significant recovery. Unexpectedly

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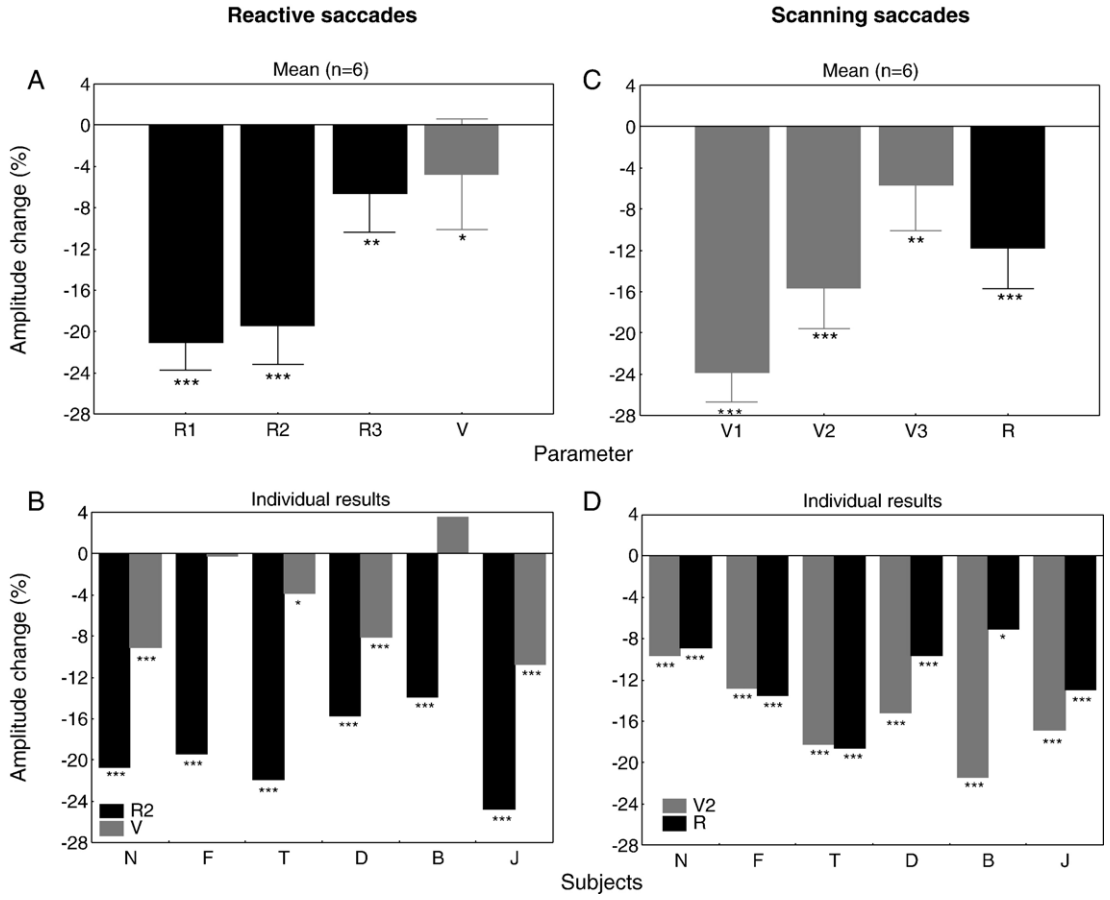

Fig. 4 – Percent amplitude change of reactive (left panels) and scanning (right panels) saccades. (A, C) Mean data ($n=6$ subjects). In each panel, bars 1–3 correspond to the amplitude changes of trained saccades computed between the pre-test and 1) the last adaptation block ('R1', 'V1' bars), 2) the first post-test performed just after adaptation ('R2', 'V2' bars), and 3) the second post-test performed after a de-adaptation session ('R3', 'V3' bars); the last bar ('V', 'R') represents the amplitude change (pre versus post) undergone by saccades of the other type. Error bars are SD. The asterisks indicate statistically significant differences: $^{*}p<0.05$, $^{**}p<0.01$ and $^{***}p<0.001$. (B, D) Individual data. As for panels above, the 'R2' and 'V2' bars correspond to the amplitude changes of trained saccades computed between the pre-test and the first post-test performed just after adaptation. The 'V' and 'R' bars represent the amplitude change (pre vs. post) undergone by saccades of the other type. Negative and positive values indicate a decrease or an increase, respectively, of the saccade amplitude between pre-test and post-test. The asterisks indicate statistically significant differences of saccade amplitude between pre-test and post-test: $^{*}p<0.05$, $^{***}p<0.001$ (*t*-test for independent samples).

however, saccade amplitude remained significantly smaller than in the pre-test, indicating that the recovery was only partial for both types of saccades (mean amount of recovery = 65%).

2.3. *Changes in saccade amplitude: intra-type transfer of adaptation*

Fig. 5 summarizes the effect of adaptation on saccades of different amplitudes (see also Table 1). The absolute amplitude changes of RS and SVS (panels A and C, respectively) are plotted against target eccentricity for each subject. As expected, the maximum change of amplitude occurred for the trained saccade (8° target) but all other saccades also exhibited an amplitude decrease (except one subject for RS). Repeated measures ANOVAs tested, separately for each saccade condition, the effect of test session and of target eccentricity on saccade amplitude. They revealed a significant main effect of the two factors ($p<0.01$) with a significant interaction only in the SVS condition ($F_{(3,15)}=9.34$; $p<0.001$). The contrast analysis (RS condition) or the post-hoc analysis (SVS condition) indicated a significant amplitude reduction after the adaptation session for all target eccentricities ($p<0.001$). We computed in each subject the amount of adaptation transfer from the 8° trained saccade to the other saccades of different amplitudes (see Experimental procedures). These values were then averaged across the 6 subjects to produce the amplitude adaptation fields of RS and SVS depicted in Fig. 5B,D. For both saccade types, the adaptation field showed a typical asymmetrical shape, being skewed toward small target eccentricities. Note that this profile was dependent on the small target eccentricity used for the trained saccade (±8°) and also on the fact that the curve was drawn through the origin. In addition, the size of the two adaptation

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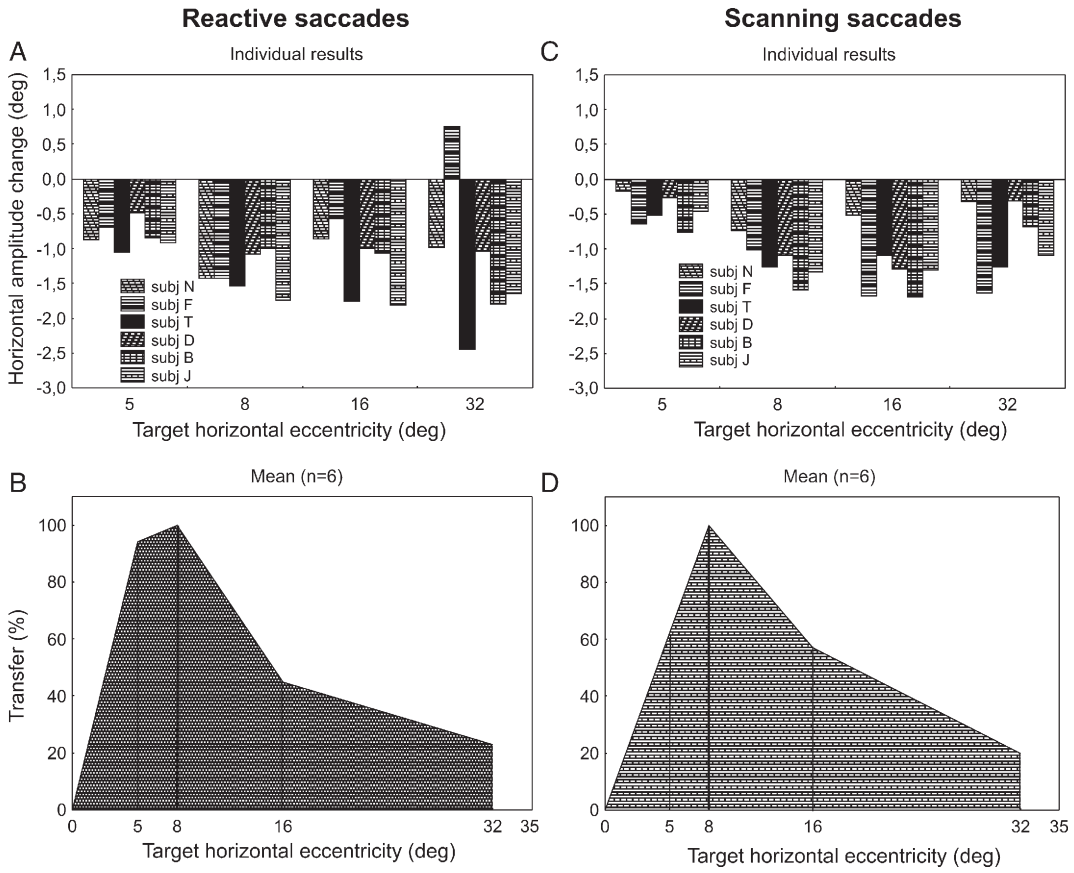

Fig. 5 – Effect of adaptation on untrained saccades. (A, C) Mean amplitude changes of the reactive (panel A) and scanning (panel C) saccades plotted for each subject and for each target eccentricity. Negative and positive values indicate a decrease or an increase, respectively, of the saccade amplitude in the post-test relative to the pre-test. The trained saccade data correspond to the +8° eccentricity; all other data refer to untrained saccades. (B, D) Adaptation field in the amplitude dimension for the reactive (panel B) and the scanning (panel D) conditions: the mean percent adaptation transfer is plotted as a function of the target eccentricity, the amount of transfer being set at 100% for the trained saccade.

fields was similar (half-height width for RS and SVS = 12° and 14°, as determined qualitatively in Figs. 5B,D).

2.4. *Changes in saccade amplitude: inter-type transfer of adaptation*

We now investigate the transfer of adaptation between saccades elicited in a reactive or in a scanning mode toward the same 8° target eccentricity. As depicted in Fig. 4B, SVS (grey bars) were significantly affected after RS adaptation in only 4 subjects (t-test for independent samples). The two other subjects (F and B) showed no statistically significant change in SVS amplitude after RS adaptation. In the scanning condition illustrated in Fig. 4D, all the subjects underwent a significant decrease of amplitude of RS (black bar) after SVS adaptation. This RS amplitude change was either similar (subjects N, F, T) or smaller (subjects D, B and J) than the trained SVS amplitude change (grey 'V2' bar). Note that the effect of SVS adaptation on RS (Fig. 4D) was much more important than the effect of RS adaptation on SVS (Fig. 4B). Thus these individual results indicate that, despite an inter-subject variability of the adaptation after-effect and transfer, as usually reported in adaptation experiments, the reciprocal transfers between the two saccade types showed a very consistent asymmetrical pattern. Present in all subjects, this asymmetrical transfer was very marked in 5 subjects and weak in only one subject (subject D). A two-way repeated measures ANOVA (type of saccade × test session) ($n=6$ subjects) was then performed in each adaptation protocol to compare the amplitude of RS and SVS in the pre-test and the post-test. In the RS adaptation protocol, we found a significant difference between the two types of saccades ($p<0.05$) and between the two tests sessions ($p<0.001$), and a significant interaction ($F_{(1,5)}=51.7$; $p<0.001$). In the SVS adaptation protocol, there was a significant effect of the test session factor ($p<0.001$), but neither the effect of saccade type ($p=0.073$) nor the interaction reached significance ($F_{(1,5)}=4.81$; $p=0.08$). Post-hoc and contrast analyses performed in the two conditions indicated that RS and SVS underwent a decrease in their amplitude ($p<0.05$) after the adaptive reduction of SVS and RS, respectively, revealing a reciprocal transfer of adaptation between the two types of saccades. However, the percent change of SVS amplitude after adaptation of RS ('V' bar in Fig. 4A: 4.8±5.6%) was much smaller than the percent change of RS amplitude following adaptation of SVS ('R' bar in Fig. 4C: 11.8±4.1%). Hence, the transfer of adaptation from RS

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to SVS (22±30%) was significantly smaller than the transfer from SVS to RS (79±27%) (repeated measures ANOVA; $F_{(1,5)}$ = 17.03; $p<0.01$). We wondered whether this asymmetrical adaptation transfer could be related to a faster de-adaptation of SVS during the post-test following RS adaptation. To this aim, we performed in each of the 6 subjects linear regressions analyses of the relation between the saccade amplitude and the trial number in post-test. No significant correlation was

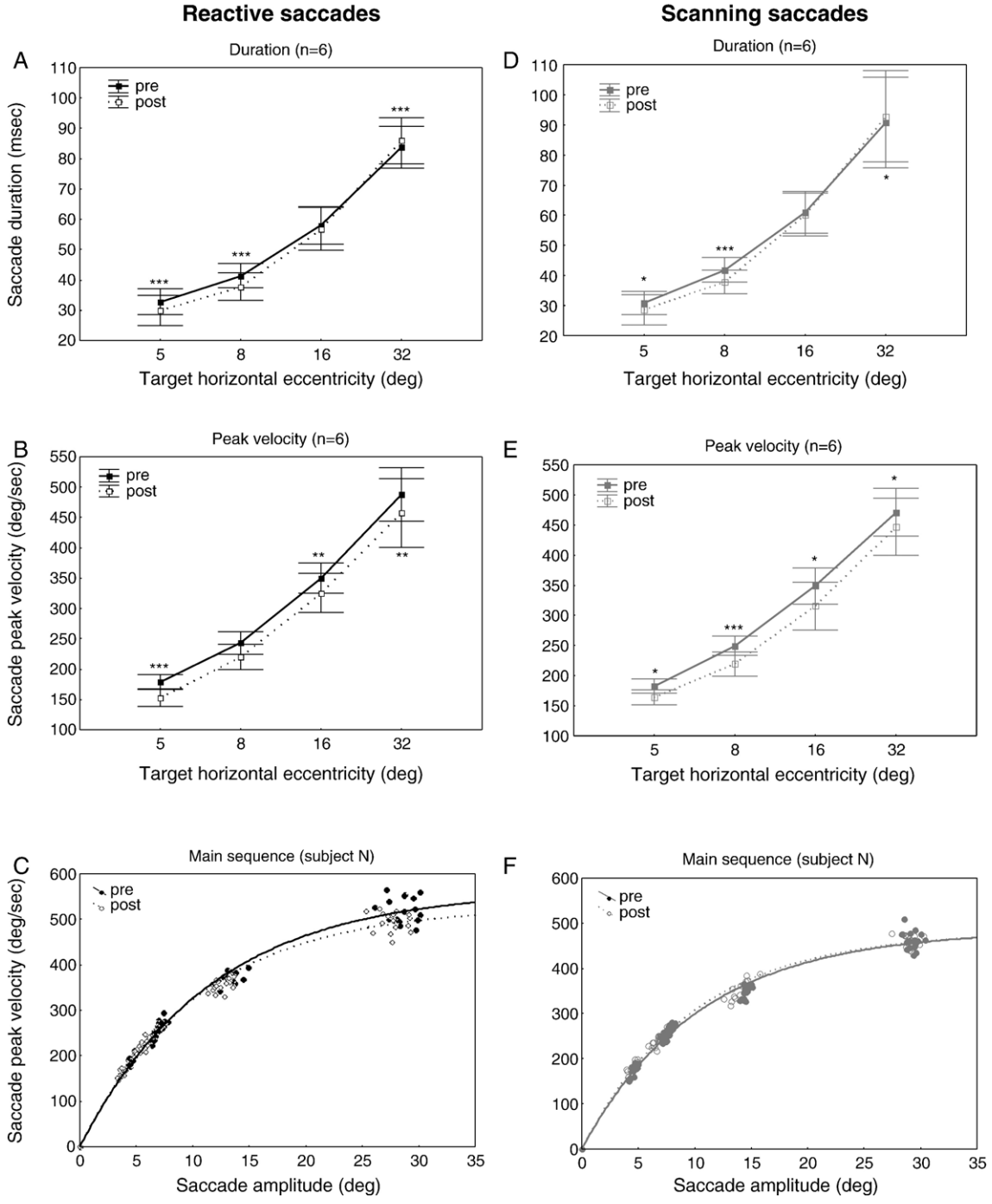

Fig. 6 – Effect of adaptation on saccade duration and peak velocity. (A, B, D, E) Mean duration (panels A, D) and mean peak velocity (panels B, E) of saccades recorded in pre-test (solid line) and in post-test (dotted line) for the trained target eccentricity (8°) and the untrained target eccentricities (5°, 16° and 32°). Reactive and scanning conditions are plotted in left and right panels. Error bars are SD. Statistically significant differences of saccade parameters between post-test and pre-test are indicated by $^{*}p<0.05$, $^{**}p<0.01$ and $^{***}p<0.001$. (C, F) Main sequence relationships for subject N in the reactive (panel C) and the scanning (panel F) conditions. Peak velocity of saccades are plotted as a function of their amplitude, in pre-test (filled circles) and in post-test (open circles). Each data point represents a saccade, the two directions of saccades being pooled together. Exponential relationships represent best-fits through the pre-test and post-test data.

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found except in two subjects (N and B; $p<0.05$) in the RS adaptation condition, but in these cases the correlation was negative and thus opposite to that expected from an effect of de-adaptation. In conclusion, the asymmetrical adaptation transfer between the two types of saccades could not be explained by a faster recovery of SVS amplitude after adaptation of RS.

2.5. *Changes in other saccade parameters (see also Table 1)*

Trained saccade latency did not significantly change following adaptation (repeated measures ANOVAs), neither for RS (post: 216±57 ms vs. pre: 247±79 ms, $p=0.24$) nor for SVS (post: 493±124 ms vs. 438±157 ms; $p=0.25$).

The saccade duration and peak velocity are depicted in Fig. 6 for the RS (panels A–C) and SVS (panels D–F) adaptation conditions. In panels A, B, D, and E, the relationships between mean saccade duration or peak velocity and target eccentricity are superimposed for the pre-test and the post-test sessions. The duration and peak velocity were submitted to repeated measures ANOVAs with target eccentricity and test session as factors, separately for RS and SVS. For saccade duration, a significant effect of the target eccentricity factor ($p<0.01$) and a significant interaction ($p<0.01$) were found for both saccade types, but a significant effect of the test session factor was found only for RS ($p<0.05$). Concerning peak velocity, there was a significant effect of both factors ($p<0.01$), without interaction ($p>0.104$), for both RS and SVS. The results of post hoc LSD Fisher tests or contrast analyses are illustrated by asterisks in Fig. 6 (panels A, B, D, and E), and revealed a pattern of changes related to adaptation (post- vs. pre-tests) remarkably similar for the two saccade types. Indeed, for small target eccentricities, including that of the adapted saccade (8°), the adaptation-related reduction of amplitude was accompanied by a decrease in both saccade duration and peak velocity. For larger target eccentricities (16° and 32°), the adaptation-related reduction of amplitude was mainly associated to a significant decrease of peak velocity (and a slight increase of duration for 32°). We next tested whether adaptation involved changes in RS and SVS dynamics by analysing for each subject the main sequence relationships. As exemplified by the results of subject N shown in Figs. 6C,F, no change in the peak velocity versus amplitude relationship was observed in post-test relative to pre-test for either type of saccades, except a small tendency of a reduced saccade velocity for the largest amplitude in the RS condition. As a quantitative test, we computed for each subject the best exponential fit of the peak velocity versus amplitude relationship (Becker, 1989) in pre-test and measured for each saccade in post-test the difference of peak velocity relative to the pre-test fit. The average across subjects revealed that the peak velocity of RS and of SVS in post-test decreased relative to the pre-test by 6±4.4°/s (i.e. 1.9%) and 6.5±8.3°/s (i.e. 2.1%), respectively. These small changes reached a statistically significant level for RS (Student's *t*-test, $p<0.05$) but not for SVS ($p=0.11$). In fact, Fig. 6C suggests that this modification was mainly due to the non-trained RS directed to the 32° target. Indeed, when restricted to the other targets, the quantitative analysis revealed a non-significant (0.74%, $p=0.23$) decrease of peak velocity. When applied to the saccade duration versus amplitude relationship, a quantitative analysis similar to the former (i.e., performed on all target eccentricities) revealed a slight (1.5%), but not significant ($p>0.11$), increase in post-test relative to the pre-test for both RS and SVS. Altogether, these analyses did not reveal, neither for RS nor for SVS, any change in the main sequence relationships specifically related to the process of adaptation.

2.6. *Effect of order of testing*

In order to avoid residual effects from a previous condition, the RS and SVS adaptations were elicited on separate days and were followed by a de-adaptation session. Nonetheless, we checked whether some residual cross-over effects could affect the results by comparing subjects who were tested in the RS condition first (group 1: subjects N, T, F) to those tested in the SVS condition first (group 2: D, J, B). In the reactive condition, an ANOVA (test session × subjects group) showed no significant difference between the two groups of subjects ($p=0.44$) nor any interaction ($p=0.2$), but a significant effect of the test session ($p<0.001$) as previously described in this study. The same ANOVA performed now in the scanning condition indicated no significant effect of the group ($p=0.84$) nor interaction ($p=0.06$), but only a significant effect of the test session ($p<0.001$) as already reported above. Thus, the subjects testing order did not affect the baseline accuracy of their pre-test saccades nor the efficacy of adaptation.

3. Discussion

The main objective of the present study was to test whether adaptation of scanning voluntary saccades (SVS) is a separate process from adaptation of reactive saccades (RS). To this aim, we compared their functional properties, and found that many of them were similar: i) adaptation is incomplete, as seen by the saturating time course of amplitude changes and by the limitation of after-effect to 39% (48.5% for RS) of the final intra-saccadic target displacement, ii) it may be subjected to fast consolidation since the de-adaptation phase performed after a short rest period did not induce complete recovery, iii) the transfer to untrained saccades depends on their amplitude according to a broad tuning function (adaptation field), suggesting a vector-specificity, and iv) adaptive changes of saccade amplitude are not accompanied by any change in the main sequence relationships. However, the adaptation transfer was strongly asymmetrical in favour of the SVS to RS transfer. In the following, we discuss these new findings and their possible neurophysiological implications.

3.1. *Magnitude of adaptation*

As already well described for RS in humans (e.g., Deubel et al., 1986; Frens and 1Van Opstal, 1994; Albano, 1996) and in monkeys (e.g. Straube et al., 1997; Scudder et al., 1998), our data showed that the time course of backward adaptation of SVS presented an initial fast phase followed by a slower phase of progressive amplitude decrease until reaching a nearly stable level at the end of the adaptation session (see Fig. 3). This steady-state level was smaller than the maximum value

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of amplitude change expected from our double-step protocol (40%). These observations thus suggest that beyond a certain limit, the mechanisms of adaptation can no longer reduce saccade amplitude, unless maybe very slowly over a much larger number of trials. Note that the time course and total amount of amplitude decrease were similar for RS and SVS adaptations. Despite this almost identical behaviour during adaptation, the adaptation after-effect measured in the post-test relative to the pre-test slightly differed between RS (−19.4%) and SVS (−15.7%), although this difference was not statistically significant. It has already been noted that the mean saccade amplitude in post-test differs from that at the end of adaptation for RS (Frens and Van Opstal, 1994; Straube et al., 1997; Scudder et al., 1998; Robinson et al., 2003; Alahyane and Pélisson, 2005). Our new finding is that this amplitude difference was also observed for SVS and was even larger than for RS (compare panels C, D to panels A, B of Fig. 3). This last observation cannot be explained by a faster recovery for SVS than for RS since we found no correlation between SVS amplitude and number of trials during the post-test. Nor can it be explained by a more labile adaptation for SVS than for RS, leading for the former to a measurable decay during the short period of time separating the end of the adaptation session and the start of the post-test. Indeed, this hypothesis predicts that the adaptation of SVS should be less resistant to de-adaptation, a prediction not verified by our results which instead revealed an equal amount of recovery for the two saccade types (65%) following the de-adaptation session. We would therefore propose a more likely explanation for the difference of retention rate between the two saccades types. We suggest that the reduction of saccade amplitude during exposure to a backward double-step target protocol involves not only true adaptive mechanisms, leading to the after-effect observed in post-test, but also other unspecific factors. Although presently unknown, these non-specific factors would be larger for SVS adaptation. Consequently the amplitude change achieved during the adaptation phase would overestimate the true level of change due to the adaptation mechanisms themselves, particularly for SVS. Therefore, in an attempt to isolate the adaptation mechanisms from potential unspecific factors, we will primarily base the following discussion on the after-effect measured during the post-test.

3.2. *Adaptation fields and main sequence*

We investigated the amount of adaptation transfer of SVS to a large range of SVS amplitudes. Our results demonstrated that adaptation of a rightward 8°-SVS transfers within a restricted but large region around this trained SVS. Note that another work from our laboratory has extended this observation to the direction dimension, revealing the existence of 2-D adaptation fields for SVS (Pélisson et al., 2005). The present study directly compared in the same group of subjects the amplitude component of adaptation fields between SVS and RS. For both types of saccades, the transfer rate decreases as the vector of the untrained saccade moves away from the adapted vector. Note that the two adaptation fields are similar, and their shape is reminiscent of that described for RS by Noto et al. (1999) in monkey and Frens and Van Opstal (1994) in humans. These data also underline that adaptation fields were very broad since the adaptation of 8° saccades influenced saccades up to 32° in amplitude, a finding that previous studies focussing on a more restricted range of amplitudes have missed. To conclude, our study confirms the notion of adaptation field previously revealed for RS in humans (Miller et al., 1981; Deubel, 1987; Frens and Van Opstal, 1994; Albano, 1996) and in monkeys (Straube et al., 1997; Noto et al., 1999; Watanabe et al., 2000) and extends this notion to SVS. Interestingly, this last observation suggests that the mechanisms underlying adaptation of both RS and SVS involve neural structures where saccades are encoded as vectors.

The decrease of saccade amplitude induced by backward intrasaccadic target steps was accompanied by a decrease of duration and peak velocity for both RS and SVS. However, the relationships between saccade duration or peak velocity and saccade amplitude (main sequences) were not modified after adaptation. A lack of modification of main sequences for backward adaptation of RS was also previously reported in humans (Frens and Van Opstal, 1994; Alahyane and Pélisson, 2005; but see Abrams et al., 1992; Straube and Deubel, 1995) but saccade dynamics following SVS adaptation have not yet been documented. Here, we demonstrate that the adaptive mechanisms of both RS and SVS primarily affected the amplitude and not the dynamics of saccades. This finding can provide clues on the possible sites where adaptive modifications take place. For RS, we suggested in a previous article (Alahyane and Pélisson, 2005) that the backward adaptive mechanisms modify signals encoded upstream from the local feedback loop of the pulse generator. Based on the present work, the same hypothesis can be proposed for backward adaptation of SVS.

3.3. *Inter-type transfers of adaptation*

Studying how adaptation transfers between RS and SVS can indicate to what extent saccadic adaptation mechanisms, and their neural substrates, differ or overlap. Our results revealed a 79% transfer from SVS to RS and a transfer of only 22% in the reverse direction. This asymmetrical transfer was observed in all 6 subjects, although it was less strong in one subject. Only four previous studies have measured the transfers of adaptation between reactive and voluntary saccades. Erkelens and Hulleman (1993) studied the transfer from SVS to RS and found a much lower value (24%). This difference with our data may be related to the paradigm they used to induce adaptation: a simple visual scene reduced to two permanent targets was submitted to a 50% intrasaccadic step and repeated in only 36 successive trials. These features may have favoured the contribution of non-adaptive factors in the development of saccade amplitude changes, and the true level of adaptation may thus have been insufficient to reveal a significant transfer to RS. In the second study (Deubel, 1995), a similar asymmetry of adaptation transfers between SVS and RS was revealed but the transfer values were weaker than ours (37% from SVS to RS and a statistically non significant 11% transfer in the reverse configuration). These smaller transfers, in particular from SVS to RS, could result from the testing and analysis methods used in this study. Indeed, blocks of untrained reactive trials were interleaved with blocks of trained SVS *during the adaptation*

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session, and the gain change of each saccade type was computed using exponential fits. With this method, the computation of the trained saccade gain change may have included the contribution of non-specific factors (see Magnitude of adaptation), leading both to an overestimation of the specific effect of adaptation and to an underestimation of the transfer amount. In the third study (Fujita et al., 2002), small amounts of transfer (25%) were again described but in this case the adaptation effect was symmetrical between the two types. These values were obtained with a method close to Deubel's (1995) in that the decrease of saccade gain *during* the adaptation phase was taken as a reference value but the gain change of the untrained saccade was measured *between post- and pre-adaptation* sessions. So again, the low values of transfer can be partly accounted for by an overestimate of the adaptive change of the trained saccade. Besides, a large intrasaccadic target jump (50%) was used, leading to potential confounding factors already mentioned above for the Erkelens and Hulleman's study. Finally, it is noteworthy that Fujita et al. actually did not study scanning voluntary saccades like in our study but rather delayed voluntary saccades toward a single predetermined target in an overlap paradigm. An overlap paradigm was also used to induce VS in the fourth study (Collins and Dore-Mazars, 2006). However, contrary to the Fujita et al.'s study, VS were not directed toward a single target but toward a set of visual symbols constituting a spatially-extended object. The same visual display was used to trigger RS, but in a gap paradigm. Interestingly, Collins and Dore-Mazars found a strong asymmetrical transfer between RS and VS in favour of VS to RS, very similar to our data. Finally, this asymmetrical transfer of adaptation has been recently confirmed in another study (Cotti et al., 2006). To conclude this paragraph, it is important to keep in mind that the amount of adaptation transfer depends both on the methodological approaches used to induce RS and VS adaptations and on the methods used to calculate the transfer. Taking into account these factors, the asymmetrical transfer of adaptation between SVS and RS reported in the present study indicates that the mechanisms underlying SVS and RS adaptation may not be as independent as previously assumed. This conclusion provides important constraints on the possible neural substrate of saccadic adaptation.

3.4. *Implications for possible neural substrates*

The adaptation vector-specificity observed for both RS and SVS suggests that modifications of motor commands during adaptation take place in neural oculomotor circuits in which movement fields have been described, like the superior colliculus (SC), the nucleus reticularis tegmenti pontis (NRTP), the paramedian pontine reticular formation (PPRF), the central mesencephalic reticular formation (cMRF), the basal ganglia or the frontal eye field (FEF) (Sparks et al., 1976; Hepp and Henn, 1983; Bruce and Goldberg, 1985; Crandall and Keller, 1985; Hikosaka and Wurtz, 1989; Waitzman et al., 1996). The lack of change in main sequence further predicts that the neural locus of adaptation is upstream from the pulse generator of the brainstem reticular formation that determines saccade dynamics. For RS, previous behavioural, neurophysiological and clinical works have suggested that adaptation takes place downstream from the SC and also involves the medio-posterior cerebellum (see Introduction). Our present data are thus consistent with this hypothesis. Concerning now the locus of SVS adaptation, contrary to our expectations (see Introduction), the present study produced two apparently contradictory sets of results. On the one hand, the similarities of most adaptation characteristics between RS and SVS would suggest that the neural substrates underlying the two types of adaptation are common. On the other hand, the asymmetrical transfer of adaptation between RS and SVS would imply that these neural substrates are at least partially separated. How can these two views be reconciled? We would like to propose two possibilities which, although speculative and non-exhaustive, may represent interesting working hypotheses for future studies. **The first possibility** is that adaptations of RS and SVS rely on two completely separate neural loci, but which both encode the vector eye displacement, upstream from the local feedback loop. For example, RS adaptation would involve a locus controlled by the medio-posterior cerebellum and located downstream from the SC but upstream from the pulse generator, whereas SVS adaptation would involve the FEF. This scheme is partly analogous to the Deubel's (1999) model, based notably on the data published by the same author (Deubel, 1995) and already discussed above. Note, however, that in order to account for the large transfer of SVS adaptation to RS demonstrated in the present study, this hypothesis is complicated since it requires a strong projection towards the FEF of signals related to RS generation. This requirement is not in accordance with a previous work showing that RS generation mainly implies the direct parieto-collicular pathway (Gaymard et al., 2003). **The second possibility** is that saccadic adaptation involves both a locus common to the two types of saccades and two separate loci recruited specifically for RS or SVS. The common locus would account for the strong similarity disclosed in the present study between behavioural properties of adaptation of SVS and RS and, given what is mentioned above, would involve brainstem neurons located downstream from the SC. The two separate loci would account for the asymmetrical transfer of adaptation between RS and SVS reported here and in other recent studies (Collins and Dore-Mazars, 2006; Cotti et al., 2006). These specific adaptation loci could reside in different structures for SVS and RS: e.g., the medio-posterior cerebellum for RS, and the FEF for SVS, as in the Gancarz and Grossberg's (1999) model. Alternatively, the specific adaptation loci could involve partially overlapping anatomical loci within the same structure (e.g., the medio-posterior cerebellum for RS and another part of the cerebellum for SVS). Because an exclusive involvement of FEF in SVS adaptation is deemed less likely (recall complication above), we favor the hypothesis of partially overlapping anatomical sites within the cerebellum (see also Pélisson et al., 2006). However, further studies using complementary neurophysiological approaches are required to directly contrast these different possibilities and to understand the relationships between putative separate adaptation loci.

In conclusion, human voluntary and reactive saccades rely on adaptive mechanisms that share many functional properties but at the same time present an asymmetrical pattern of transfers. These adaptive mechanisms may involve a network including a common brainstem site and neural populations

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which are specifically recruited for RS and SVS. Complementary neurophysiological studies comparing the two types of adaptations are necessary to clear up these substrates.

4. Experimental procedures

4.1. *Subjects*

The experiment was conducted in six participants (3 authors; age 22–48 years). All subjects had a normal or a corrected to normal vision and provided their informed consent before the recording sessions. The study complied with the declaration of Helsinki.

4.2. *Apparatus*

Participants were sitting in a dimly illuminated room with their head stabilized by a chin rest and a cheekbone rest, facing a fast video screen controlled by a VSG (Visual Stimuli Generation) system (CR, Cambridge, UK). They were required to precisely follow with their eyes the visual targets presented on the video screen located at a 57 cm distance. Targets were black circles (6 mm diameter) on a grey background.

4.3. *Protocol*

Both leftward and rightward saccades were adapted in the same session, using a backward adaptation protocol. Every subject underwent both SVS and RS adaptation protocols, performed on 2 separate days (as illustrated in Fig. 1 for the rightward direction).

4.3.1. *Reactive condition (Fig. 1A)*

4.3.1.1. *Adaptation session.* Saccadic adaptation was induced by the double-step target protocol introduced by McLaughlin (1967) and described in our previous papers (e.g. Alahyane et al., 2004).

A central fixation point (FP) was turned on for a pseudo-random period (1300 or 1500 or 1700 ms). Then, FP was replaced by a peripheral target (T1) which was randomly presented at 8° to the right or to the left (±8°). This sudden step of the target from FP to T1 elicited a horizontal RS during which T1 was shifted backward to T1′. This intrasaccadic target step corresponded to 25% of the initial target displacement at the beginning of the adaptation session (144 trials), and to 40% at the end of this session (96 remaining trials). The rationale of progressively increasing the backward step amplitude was to increase the amount of saccadic adaptation without inducing a conscious perception of the intrasaccadic step by the subjects. Target T1′ was switched off 800 ms after its presentation and a sound occurred 500 ms later to require the subjects to fixate at the center of the screen. About 2 s after peripheral target presentation, the central FP re-appeared, indicating the start of the next trial. The adaptation session was divided into 5 blocks of 48 trials (24 leftward saccades randomly intermingled with 24 rightward saccades), with a 25% and 40% intrasaccadic target jump for blocks 1–3 and 4–5, respectively.

4.3.1.2. *Test sessions.* The effect of adaptation was tested by recording RS in single-step trials before (pre-test) and after (post-test) the adaptation session. For most single-step trials, the fixation point FP was presented at the center of the screen for a pseudo-random duration (1300 or 1500 or 1700 ms) and then replaced by a peripheral target T1 located at one of six possible positions relative to FP (±5°, ±8° and ±16°). For the two additional trial types (±32° target eccentricity), FP was located at −16° (left) or +16° (right) relative to the center of the screen and T1 at +16° or −16°, respectively. In all trials, the sudden target step from FP to T1 elicited a horizontal RS during which T1 was extinguished, to avoid any de-adaptation (i.e., recovery of saccade amplitude) in the post-test session. Then, 500 ms after the extinction of T1, a beep sounded to require the subjects to look at the center of the screen. The next trial began by FP presentation, 1800 ms after the presentation of the peripheral target. The 8° trials were presented in a separate block (12 repetitions per direction, the two directions being randomised) while the 5° and 16° eccentricities were interleaved in a pseudo-random order in another block of trials (8 repetitions per amplitude and direction). This block also included the 32° trials, with eight trials (four per direction) at the start and at the end of this block, respectively. The transfer of adaptation to the other type of saccades (SVS) was also tested for the trained amplitude (±8°; 12 trials per direction) in another block of trials.

4.3.2. *Scanning (voluntary) condition (Fig. 1B)*

A modified double-step target protocol, adapted from that of Deubel (1995), was used to induce backward adaptation of SVS. In all sessions (adaptation and test), subjects had to scan at their own pace a series of visual targets presented simultaneously. To insure attentive fixation of each target, subjects were asked to discriminate grey stimuli located inside the targets. The stimuli could be either a complete letter 'E' or a truncated version of this letter with 2 pixels missing. Subjects had to report the number of truncated symbols they have seen in the visual scene.

4.3.2.1. *Adaptation session.* During each trial, subjects performed a 4° vertical saccade followed by three 8° horizontal SVS to explore a set of five targets presented for 4 s. Four targets were arranged in a horizontal row with a regular spacing of 8°, the first one being positioned either at −8° from the screen center or at +8°, to elicit rightward or leftward SVS, respectively. The fixation point (FP) was located 4° above this left-most or this right-most target of the horizontal row. Subjects had to initially fixate FP. After 1600 ms, a surrounding circle was added to FP and simultaneously the four additional targets were presented. Only when the circle disappeared 500 ms later, were subjects allowed to scan the four remaining targets, performing first a downward saccade, then a sequence of 3 horizontal saccades ('I', 'II', 'III' in Fig. 1B). Note that the 3 horizontal saccades were executed by subjects at their own pace and can thus be considered as SVS whereas the vertical saccade was triggered both on external (disappearance of the circle around FP) and internal cues. Because adaptation of horizontal saccades does not transfer to vertical saccade and vice versa (Deubel, 1987), this arrangement allowed us to

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minimize any potential interaction between RS and SVS. As soon as horizontal eye velocity exceeded a 100–150°/s threshold during each of the three horizontal SVS, the entire target set was shifted horizontally backward in order to induce an adaptive decrease of the SVS amplitude. Thus during saccade I, the scene was displaced to the left from FP–T4 positions to FP′–T4′ positions; it was displaced a second time toward FP″–T4″ positions during saccade II, and a third time toward FP‴–T4‴ locations during saccade III. The amplitude of these intra-saccadic displacements represented 25% of the initial SVS desired amplitude in the first 48 trials (i.e. 144 saccades) and 40% in the last 32 trials (i.e. 96 saccades). At the end of the trial, subjects indicated the number (0, 1 or 2) of truncated letters they have detected in the sequence by pressing a button (the actual number and position of truncated symbols varied randomly between trials). The next trial started immediately after the manual key press. The adaptation session was composed of 5 blocks intermingled with rest periods of about 1 min. Each block contained 8 trials (i.e., 24 horizontal SVS) in the rightward direction followed by 8 trials in the leftward direction, blocks 1–3 and 4–5 containing trials with a 25% and a 40% intrasaccadic target step, respectively.

4.3.2.2. Test sessions. Trials during the pre- and post-test sessions differed from adaptation session trials on two aspects (Fig. 1B). First, the visual scene contained only 3 targets, eliciting a downward saccade from FP to T1 and a horizontal SVS from T1 to target T2. Second, the whole display did not jump backward during the horizontal SVS but instead disappeared in order to prevent de-adaptation in post-test. The vertical saccade was always 4° in amplitude whereas the amplitude of the horizontal saccade was varied by presenting target T2 at different eccentricities from T1: ±8° in a block (12 rightward trials followed by 12 leftward trials), and ±5°, ±16° and ±32° in another block (8 repetitions per amplitude and per direction). The ±5° and ±16° eccentricity trials were grouped by direction but not by amplitude. Concerning the 32° eccentricity trials, half was presented at the start of this block and the remaining half at the end. In all trials, only the target located below FP contained a normal or a truncated letter that the subject had to discriminate. The number of truncated symbol (0 or 1) was reported by the subject by means of a button-press at the end of the trial. The next trial started immediately afterwards. At last, the transfer of adaptation to the other type of saccade (RS) was also tested for the trained amplitude (±8°; 12 trials for each direction, in a random order).

4.3.3. Temporal order of adaptation protocols and of blocks of trials

Each of the six subjects was tested in the two protocols several days apart (except subject J: a single day apart). Three subjects (N, T, F) underwent the reactive protocol first whereas the other three subjects (D, J, B) underwent it secondly. In order to avoid possible cross-over effects between two successive protocols due to long term retention of adaptation (Alahyane and Pélisson, 2005), and to favor the recovery of saccade amplitude, a session of de-adaptation was performed immediately after each adaptation protocol. In this de-adaptation session, 4 blocks of 60 saccades each (30 rightwards and 30 leftwards) were performed in trials identical to those of the adaptation session except that the visual scene or target did not jump during the saccade (visual stimuli remaining stable for 4 s or 2 s in the scanning and the reactive conditions, respectively). To minimize fatigue by reducing the overall duration of wearing the eye-movement-recording system, eye movements were not recorded during de-adaptation sessions. Finally, the efficacy of de-adaptation was checked for the ±8° trained saccade in a final test session, according to a protocol strictly identical to that described above.

In summary, for each type of saccades (reactive and scanning), subjects were submitted to the following schedule:

1) Pre-test: block A: saccades of the same type as the trained saccade (±8° RS or ±8° SVS) but of different amplitudes (±5°, ±16°, ±32°; 48 trials), then block B: saccades of the other type (SVS or RS) but of the same amplitude (±8°; 24 trials), and finally block C: saccades of the same type and amplitude as the trained saccade (±8° RS or ±8° SVS; 24 trials),
2) Adaptation session divided into 5 blocks (±8°; 240 trials) for trained saccades (RS or SVS),
3) First post-test: block C, then block B and finally block A (identical to pre-test blocks seen above),
4) Pause of 10–20 min outside the experimental room,
5) De-adaptation phase divided into 4 blocks (±8°; 240 trials) for trained saccades (RS or SVS),
6) Second post-test: block C only.

The whole procedure until the pause lasted about 50 min, followed by a 15- to 20-min de-adaptation phase and a 3-min post-test.

4.4. *Eye movement recording, visual stimulation and data acquisition*

A helmet-mounted pair of infra-red sensors allowed recording of the horizontal and vertical movements of each eye (*EyeLink II* video-oculographic system, SR-Research, Canada), at a frequency of 500 Hz with an accuracy better than 0.5°. Just before the recording session on each day, a calibration was performed by requesting subjects to sequentially look at 9 targets constituting a rectangular array of 28° height and 38° width and centred on the center of the screen. An in-house PC program processed on-line the position of the left eye (low pass filtering, differentiation and thresholding) and produced a TTL trigger signal whenever the horizontal velocity exceeded a threshold of about 100–150°/s. This signal triggered the jump or the disappearance of the visual display presented on the high speed video monitor, in the adaptation or test sessions, respectively. Changes of visual display were achieved by a real-time interface within 10 ms of threshold detection. The same program sampled and recorded eye position data (sampling frequency = 1000 Hz) for off-line analyses while another in-house computer program controlled the presentation of the visual targets.

4.5. *Data analysis*

The horizontal and vertical components of the two eyes were analysed off-line. After filtering (100 Hz cut-off frequency finite impulse response (FIR) filter), the initial and final

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positions of all saccades were marked on the basis of a velocity threshold of 40°/s. These two markings were checked by the experimenter and could be manually changed. Only primary saccades were further considered. Analyses were performed on the data of the cyclopean eye data taken as the average of the right eye and left eye data. Trials with a primary saccade latency <100 ms or >1000 ms or trials with a saccade that was not correctly detected on-line or contaminated with a blink were eliminated. Also, in the SVS condition, trials in which the discrimination was erroneous were excluded from the analysis (representing only 1.3% of SVS trials). The overall amount of eliminated saccades represented 4.3% of all saccades collected. We analysed only the horizontal primary saccades, discarding in the SVS condition the initial vertical saccades directed toward the first target.

The following parameters were computed for each primary saccade and for each subject. Saccade amplitude was computed as the difference between the initial and final positions of the eye, and saccade duration was obtained as the corresponding time difference. Mean saccade gain corresponded to the ratio between mean saccade amplitude and target eccentricity. The absolute amplitude change related to the adaptation protocol was calculated as the difference between the mean post-test amplitude and the mean pre-test amplitude. The relative amplitude change (percent amplitude change) was calculated as follows: [(absolute amplitude change)/(mean pre-test amplitude)]*100. The amount of adaptation transfer corresponded to: [(mean percent amplitude change of untrained saccades)/(mean percent amplitude change of the trained saccade)]*100. The latency of RS was the delay between target onset and primary saccade onset. For the SVS condition, the so-called 'latency' corresponded to the duration of each preceding fixation (i.e., to the fixation duration of T1 for the test sessions; see right panel of Fig. 1B).

Statistics were performed by analyses of variance (ANOVAs), followed by post-hoc LSD Fisher tests or contrast analyses (see Results for details). Significance level was set at $p<0.05$.

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