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Spatial transfer of adaptation of scanning voluntary saccades in humans

Running head: Adaptation fields of voluntary saccades

Nadia **Alahyane**^{a,b}, Anne-Dominique **Devauchelle**^{a,c}, Roméo **Salemme**^a, Denis **Pélisson**^a

^aINSERM, U864, Espace et Action, Bron, F-69500, France; Université de Lyon, Lyon, F-69003, France ; Université Lyon 1, Biologie Humaine, Lyon, F-69003, France; IFR19, Institut Fédératif des Neurosciences de Lyon, Lyon, F-69003, France

^bPresent address: Centre for Neuroscience Studies, Queen's University, Botterell Hall, Room 234, Kingston, Ontario, K7L 3N6, Canada

^cPresent address: INSERM/CEA/Université Paris 11, U 562 Neuroimagerie Cognitive, Service Hospitalier Frédéric Joliot, Orsay cedex, F-91401, France

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Please address Correspondence and Requests for reprints to:

Nadia Alahyane

Centre for Neuroscience Studies

Queen's University, Botterell Hall, Room 234

Kingston, Ontario, Canada, K7L 3N6

Phone: (1) 613-533-6000 (poste 75216)

Fax: (1) 613-533-6840

E-mail: nadia@biomed.queensu.ca

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Abstract

The properties and neural substrates of the adaptive mechanisms which maintain over time the accuracy of voluntary, internally-triggered, saccades are still poorly understood. Here, we used transfer tests to evaluate the spatial properties of adaptation of scanning voluntary saccades. We found that an adaptive reduction of the size of an horizontal rightward 7° saccade transferred to other saccades of a wide range of amplitude and direction. This transfer decreased as tested saccades increasingly differed in amplitude or direction from the trained saccade, being null for vertical and leftward saccades. Voluntary saccade adaptation thus presents bounded, but large, adaptation field, suggesting that at least part of the underlying neural substrate encodes saccades as vectors.

Keywords: man, eye movement, oculomotor, voluntary saccade, eye displacement vector, plasticity, transfer.

Introduction

Understanding and acting on our environment crucially depend on basic behaviours such as saccadic eye movements. Most of the saccades we perform daily are used to scan our stable visual environment. These internally-triggered, voluntary saccades (VS), usually remain accurate throughout life thanks to adaptation mechanisms that compensate for systematic saccadic errors. A similar adaptation of VS can be experimentally induced over a short time-scale (some tens of minutes in human) [1-3]. In this case, the whole visual scene is systematically displaced during every VS, without conscious detection by the subjects (due to saccadic suppression [4]), to induce artificial post-saccadic errors.

Despite their significance in daily life, knowledge of the adaptive mechanisms of VS is hitherto sparse in comparison to those of reactive saccades [for review 5] and the existence of common adaptive mechanisms for both saccades types is highly debated [1-3, 10-12].

Reactive saccades are automatically triggered by the sudden presentation of a novel visual target in the environment. Adaptation of these reactive saccades is restricted to a field around the adapted saccade vector and in this “adaptation field” [6], it decreases for untrained saccades as their vector (amplitude or direction) is increasingly different from the trained saccade vector. An obvious manifestation is the null transfer from horizontal to vertical saccades [7] or between rightward and leftward saccades [8,9].

Our goal was to examine if adaptation of VS also presents adaptation fields, which will help determine if the adapted neural signals encode VS as vectors or as their horizontal and vertical components. We previously found that adaptation of a given horizontal VS affects other horizontal VS within a limited range of amplitudes [2]. We extended this approach here by testing the transfer of VS adaptation to a large range of VS amplitudes and directions. Part of results has been presented in an abstract form [13].

Methods

Eight subjects (A-H) with a normal or a corrected-to-normal vision (age 22-60; 3 authors) volunteered in this study. The study was conducted in accordance with the declaration of Helsinki, with methods detailed in [2].

Design and procedures

Subjects sat in a dimly illuminated room with their head stabilized by a chin rest, facing a Visual Stimuli Generation system (CRS, Cambridge, UK) located 57 cm away.

The experimental session comprised a pre-test run, an adaptation run and a post-test run.

Figure 1 near here

Adaptation run. At the start of each trial, 7 targets describing two horizontal rows were simultaneously presented for 4 s (Fig. 1A). Subjects had to initially fixate a point (FP, surrounded by a circle) located randomly at $H-12.5^\circ/V2^\circ$ or $H-8.5^\circ/V2^\circ$ (equal probability) ($H-12.5^\circ/V2^\circ$, for instance, indicates a position at 12.5° to the left and 2° above the screen centre). When subjects pressed a 'ready' button, data acquisition started and the circle around FP disappeared. Subjects then scanned at their own pace the six remaining targets, performing a sequence of alternating vertical and horizontal voluntary saccades (VS), without target omission or regressive movement. During each of the three horizontal VS (Fig. 1A) the entire display was shifted horizontally backward by 1.75° , i.e. 25 % of the desired VS amplitude (7°). To insure attentive fixation of all targets, subjects were asked to discriminate stimuli located inside the targets and to report their number at the end of each trial by means of key press (see [2]). The adaptation run consisted of 2 blocks of 40 trials separated by a short rest period, namely 240 rightward VS in total.

Test runs. Identical pre- and post-test runs were performed to quantify the trained VS and several untrained VS differing in amplitude or direction.

Trials were of 3 types: horizontal trials where a horizontal VS was produced after the first, downward, saccade; oblique trials where an oblique VS followed the downward saccade; vertical trials where a vertical VS was elicited after the first, horizontal and leftward, saccade (Fig. 1B). All trials started with the presentation of FP and 2 seconds later, of a circle around FP and two additional targets (T1 and T2). After pressing a 'ready' button subjects

performed at their own pace two saccades to fixate T1, then T2. In horizontal and oblique trials, FP was positioned at H-7.25°/V2° and T1 was always located below FP at H-7.25°/V-2°. In horizontal trials, T2 was presented along the same horizontal meridian as T1 but at different eccentricities (-7°, 4°, 7°, 14° and 24°). In oblique trials, T2 was always located at 7° to the right of T1 but at six different directions relative to the horizontal meridian (+/-15°, +/-30° and +/-60°). Finally in vertical trials, FP was presented at H-7.25°/V-2° and T1 at H-14.25°/V-2°; T2 was located randomly at H-14.25°/V5° or H-14.25°/V-9° to test upward and downward vertical VS, respectively. In all trials, the whole display was blanked upon detection of the VS from T1 to T2 to prevent de-adaptation, and the subjects then reported their discrimination response by means of key press (see [2]). Each pre-test and post-test consisted of 120 trials: 25 horizontal trials (5 pseudo-random repetitions per eccentricity), 30 oblique trials (5 pseudo-random repetitions per direction), 25 horizontal trials, 30 oblique trials and 10 vertical trials (5 upward interleaved with 5 downward). A short rest period was provided between each block. Note that subject A did not perform the block of vertical trials.

Data collection and analysis

Eye movements were recorded by an EyeLink video-oculographic system (SMI, Teltow, Germany) at a 250 Hz frequency and a spatial resolution of 0.05°. A real-time interface allowed visual stimulation changes (shift in adaptation run, disappearance in test runs) to take place within 10 ms of eye saccade detection (100-150°/sec velocity threshold). Another computer program (Data Wave, Longmont, USA) controlled target presentation and sampled eye position at a 500 Hz frequency. Off-line analyses, performed on the left eye signals, were restricted to primary saccades of a 100 ms to 1000 ms latency. In the adaptation run, we analysed only the 3 horizontal VS. In test runs we analysed horizontal, oblique or vertical saccades elicited between targets T1 and T2.

For each subject, we computed the following parameters: saccade radial amplitude = square root (horizontal component amplitude² + vertical component amplitude²); absolute change in amplitude = difference of mean radial amplitude between the post-test and the pre-test;

relative change in amplitude (or percent amplitude change) = [(absolute amplitude change) / (mean pre-test amplitude)]*100; amount of adaptation transfer = [(mean percent amplitude change) / (mean percent amplitude change of the trained saccade)]*100. Repeated measures ANOVAs and post-hoc LSD Fisher tests were performed on VS radial amplitude.

Results

General observations. As shown in Fig. 1C in a representative subject, the horizontal amplitude of primary VS (black circles) progressively decreased during the adaptation run. In post-test, VS remained significantly hypometric by comparison with the pre-test (grey circles 'Pre' and 'Post', independent-samples t-test, $p < 0.001$). Across all subjects, the mean reduction in saccade amplitude between pre-test and post-test reached $0.86 \pm 0.07^\circ$ (relative amplitude change = $-11.8 \pm 0.8 \%$).

Figure 2 near here

Transfer of adaptation: amplitude test. All 8 subjects exhibited a quite similar reduction of amplitude for the trained rightward 7° VS, as shown by negative values in Fig. 2A. The untrained rightward VS also showed an absolute amplitude decrease that was of greater magnitude as target eccentricity increased (except subject H for 14° and 24°). In contrast for leftward VS (-7°), the adaptation effect was highly variable and the average trend across all subjects was small. There was a significant effect of the two within-subject ANOVAs factors "test run" (pre vs post) and "target eccentricity" ($p < 0.001$) and a significant interaction ($F_{(4, 28)} = 11.2$; $p < 0.001$). All post- versus pre-test comparisons were significant (post-hoc tests, $p < 0.001$) except for the -7° VS ($p = 0.59$). We then computed for each subject the amount of adaptation transfer of the 7° rightward VS to the rightward VS (100% by definition for the trained VS) and averaged the data across subjects to yield the adaptation field plotted in Fig. 2B. A complete transfer of adaptation was observed for the 4° VS (the actual amount of transfer was $114 \pm 8 \%$ but the relative amplitude change was not significantly different from that of the 7° VS; paired t-test, $n = 8$; $t = -1.31$, $p = 0.23$). Note that, contrary to the *absolute*

amplitude changes plotted in Fig. 2A, the *relative* changes expressed by these transfer values gradually decreased for larger untrained VS, reaching 46% for the largest eccentricity tested.

Transfer of adaptation: direction test. The radial amplitude was reduced in post-test with respect to pre-test (except for subject D at 30° and 60°) and this reduction was negatively related to target direction (Fig. 2C). A significant effect of both “test run” and “target direction” (0°, 15°, 30°, 60°) factors was revealed ($p < 0.001$) as well as a significant interaction ($F_{(3, 21)} = 5.24$; $p < 0.01$). In fact only the difference between the 0° and 15° directions in pre-test was non-significant (post-hoc tests, $p = 0.34$). For untrained vertical VS, the large inter-subject variability depicted in Fig. 2C suggests a lack of systematic modification. Indeed in a second ANOVA only the interaction between the two factors “test run” and “target direction” (0°, 90°) was significant ($F_{(1, 6)} = 6.36$; $p < 0.05$), vertical VS amplitude being similar between pre-test and post-test (post-hoc tests, $p = 0.97$). The amount of transfer decreased as a function of the VS direction (Fig. 2D), falling below 40% for directions larger than 30° and completely disappearing for the vertical direction (i.e. 90°; the amount of transfer was deemed to be null because no significant difference between pre-test and post-test was found; see above).

Discussion

We found that adaptation of a rightward 7° VS transferred to saccades of a large range of amplitudes and directions. The fact that the *absolute change in saccade amplitude* increased with larger horizontal target eccentricities (Fig. 2A) could suggest that VS adaptation resulted from a parametric gain adjustment. In this case however, the *relative amplitude change* (and *adaptation transfer*) should be constant for all target eccentricities. This prediction is clearly not supported by our data since the adaptation transfer decreased as the target eccentricity increased (Fig. 2C). Thus our study confirms that VS adaptation does not generalize to VS of all sizes [2]. Instead, adaptation transferred within a restricted, albeit large, region around

the trained VS. Within this adaptation field, the transfer rate decreased as the vector of the untrained saccade moved away from the adapted vector, being null for vertical and leftward VS. **The fact** that the amount of VS adaptation and its transfer **varied** between participants is reminiscent of the large **inter-subject** variability regularly found in previous adaptation experiments for reactive saccades [for review 5]. The adaptation field was very broad in the amplitude dimension since 46% of adaptation of 7° VS transferred to 24° VS, confirming our previous study reporting a significant transfer from 8° VS to 32° VS [2]. In this same previous work, both reactive saccades and VS showed a large and similar adaptation field in the amplitude dimension. A new feature here relates to the direction dimension of VS adaptation field which was also found to be very broad. Indeed adaptation of 7° VS significantly influenced VS up to +/-60° in direction. One could argue that this wide transfer was related to the fact that the oblique VS and the trained VS had the same horizontal component. Yet the lack of a complete transfer to different oblique VS having the same horizontal component suggests that the presence of the vertical component reduced the rate of transfer. In other words, adaptation of VS likely affected the saccade vector rather than its components. A study of reactive saccades in monkey also showed an incomplete adaptation transfer (~55%) from 15° horizontal saccades to untrained saccades of same horizontal component but with a 10° vertical component (direction ~ 33°) [14]. In human, adaptation of horizontal reactive saccades significantly affected saccades along a 45° direction [6], the trained and untrained oblique saccades having the same radial amplitude instead of the same horizontal component.

Our data provide direct evidence that VS adaptation is both amplitude- and direction-specific and at the same time that this spatial specificity is broad as shown by the large size of adaptation field. These properties are shared by adaptation of reactive saccades [2,5] suggesting that the neural substrates underlying adaptation of both saccade types are, at least partially, similar (see detailed discussion in [2]). Overall our study strongly suggests that, as for reactive saccades [for review 5], adaptation of VS takes place at a locus where saccades are encoded as vectors. This locus might be located upstream from the horizontal

burst generator of the paramedian pontine reticular formation and the vertical burst generator of the mesencephalic reticular formation [15,16]. Elucidating which neural structures that project to these burst generators and that encode saccades as vectors, such as the frontal eye fields [17] or the superior colliculus [18], participate in VS adaptation will require direct neurophysiological or clinical approaches.

Conclusion

VS adaptation is still very little explored nowadays as compared to reactive saccade adaptation. Our study revealed that adaptation of VS, like that of reactive saccades, exhibits eye displacement vector specificity, suggesting that both adaptation types rely on partly common neural processes.

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Figure legends

Figure 1

A- Adaptation run. Subjects scanned a set of 6 visual targets by starting at the fixation point (FP) and making a sequence of 3 vertical 4° voluntary saccades (VS) intermingled with 3 horizontal 7° VS. During each horizontal VS, the whole visual display was displaced by 1.75° in the backward direction (small arrows). **B-** Test runs. Subjects explored a set of 3 targets: FP, T1 and T2. Test runs comprised : i) horizontal trials where a downward VS from FP to T1 (grey arrow) was followed by a horizontal VS from T1 to T2 (T2 at 4°, 7°, 14°, 24° to the right of T1, or at -7° i.e. 7° to the left of T1); ii) oblique trials with a downward VS from FP to T1 (grey arrow) followed by an oblique VS from T1 to T2 (T2 at a +/-15°, +/-30° or +/-60° direction relative to the horizontal axis); iii) vertical trials where the first VS was leftward (grey arrow) and the second one was vertical in the upward or downward direction (+/-90°). For all 3 trials types, the whole target set disappeared during the second VS. **C-** Time course of primary saccade amplitude during the adaptation run in subject F. Each black dot represents a single voluntary saccade. The mean amplitude in pre-test (Pre) and in post-test (Post) are also plotted (grey circles, error bars : standard deviations). *** p<0.001 (post-test versus pre-test).

Figure 2

A, C- Mean absolute changes in saccade radial amplitude for each subject (A-H) in the horizontal (panel A) and in the oblique and vertical trials (upward and downward trials pooled together) (panel C). Negative (positive) values indicate a decrease (increase) in saccade amplitude in the post-test relative to the pre-test. The trained saccade data correspond to the 7° eccentricity in panel A and to the 0° direction in panel C; all other data refer to untrained saccades. **B, D-** Adaptation fields: the mean percent adaptation transfer across 8 subjects is plotted as a function of target eccentricity (panel B) or of target direction (panel D). Error bars are standard errors of mean.