Vestibular information contributes to update retinotopic maps

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IN order to investigate the contribution of the vestibular system to spatial orientation, we studied memory-guided saccades in three conditions: visual-memory guided saccades (ViC), saccades to the remembered spatiotopic position of a visual target, after whole-body rotation (SVeC) and saccades to the remembered retinotopic position of a visual target, after whole-body rotation (RVeC). Visual feedback presented after each trial allowed eye position correction. The error was larger in SVeC, but the performance improved throughout the experiment (learning) in that condition only. As learning occurred over the first four trials, we omitted these trials from the average computation, and the significant difference between the conditions disappeared. It is concluded that vestibular information does contribute to update the internal spatial representation of visual information when a visual feedback is provided. *NeuroReport* 10:3479–3483 © 1999 Lippincott Williams & Wilkins.

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Introduction

During eye–head and body orienting movements, the brain needs to constantly update the internal representation of egocentric visual space by combining the visual information to the current eye and head movements [1–3]. This process implies multimodal integration of sensory and motor signals, including the efferent copies [4,5]. In order to better understand how the sensory signals are used in spatially oriented behaviors, experiments have been performed using delayed reaction tasks [6]. The closest to the present experiment is the visual memory-guided saccade task, first used with monkeys [7], which uncovered the role of the prefrontal cortex in visual representational memory [8], and then with human subjects [9]. Recent behavioral studies have shown that vestibular information can also be stored and used by the oculo-motor system to reproduce a body displacement [10–12]. This means that vestibular velocity signals (the output of the semi-circular canals is angular velocity) are time integrated and stored as body displacement to be used for further sensorimotor orientation.

From these observations, we could hypothesize that the same vestibular integration might take place to update a retinal error when moving the head or the body. Surprisingly, Blouin *et al.* [13–15] have shown that vestibular inputs are inaccurately integrated in the task of updating visual representation.

These results suggest that the vestibular system cannot be used for spatial computation. With whole-body motion in stimulus and response, it is possible to use the contingent somatosensory and temporal information, to reproduce at least some of the kinematic parameters. For real gaze orientation, however, the direction in which to look has to be computed, not reproduced.

Our purpose was to investigate in human subjects the updating mechanism of the retinotopic map based on vestibular information. The novelty of our study was to compare the ocular position accuracy to a memorized visual target when the vestibular input was taken into account to update the retinal error or when the vestibular input was ignored in order to maintain constant the retinal error. Visual feedback was provided at the end of each trial to make possible the eye position correction.

Materials and Methods

We studied horizontal saccades to visual memorized targets in five healthy subjects. The subject was seated in the dark in a motorized chair which could rotate about the vertical axis. Horizontal and vertical eye movements were recorded by DC current electro-oculography. All subjects gave informed consent to participate in the study, which was accepted by the local ethic committee.

The subject had to maintain gaze on a head-fixed visual fixation point (P) straight ahead for 7.5 s while a visual target was flashed (F) for 1 s on the horizontal axis. This was shared by all the three conditions of the experimental paradigm. In the visual condition (ViC), after the extinction of the fixation point P, the subject had to perform ocular saccades to the location of the previously seen visual target F, in the current stationary body orientation. In this condition, F was randomly 10 or 20°, right or left. In the spatiotopic-vestibular condition (SVeC), a chair velocity step rotation (acceleration 100 deg/s^2, peak velocity 10 deg/s) was applied while the subject was fixating the head-fixed visual point P (VOR suppression). After the chair was stopped and the fixation point P was switched off, the subject had to saccade to the location in space of the previously seen target F. Chair rotation was 10, 20 or 30° rightward (CW) and F was 10° right. In the retinotopic-vestibular condition (RVeC), a chair velocity step rotation was applied while the subject fixated the head-fixed visual point P as in condition SVeC. After the chair was stopped and the fixation point P was switched off, the subject had to saccade to the retinotopic location of the previously seen target F. Chair rotation was 10, 20 or 30° rightward (CW) and F was 10 or 20°, right or left.

In each condition, after the ocular saccade(s) had been made, a visual target was presented in the true location where the subject should be gazing and the subject made, if necessary, a corrective saccade. The three different experimental conditions were presented in different sequential orders.

We calculated the gain and the absolute error of the ocular position (E) before the corrective saccades. For each parameter, statistical analysis was performed by one-way repeated measured ANOVA (within subject factor condition: ViC, RVeC and SVeC). *Post-hoc* comparison was realized by using Student–Newman–Keuls test. A linear regression analysis was computed to determine the correlation between the target position (F) and E and between E and head rotation amplitude (H). The significance level was established at a 95% confidence interval.

Results

The preliminary data observation revealed that performance was fairly accurate in all conditions (Fig. 1).

Regression: The linear regression between F and E in ViC had a slope of 1.04 ± 0.07 (mean $\pm$ s.d.), the intercept was $-0.43 \pm 0.45°$, and r^2 was 0.98 ± 0.01. In RVeC the slope was 1.08 ± 0.06, the intercept $-0.29 \pm 1.41°$, and $r^2 = 0.98 \pm 0.01$; while the intercept variability was larger in RVeC than in ViC, it should be noted that there was no correlation between H and E, in RVeC, suggesting that subjects responses were not influenced by body rotation. Finally, in SVeC there was no correlation between F (10° right) and E, or between H and H + E (eye in space) but there was between H and E: the slope was 0.95 ± 0.10 and the intercept $8.36 \pm 0.99°$, i.e. fairly close to the 10° expected. However, r^2 was 0.83 ± 0.08 and was, therefore, smaller in SVeC than in both other conditions.

Gain: Computation of the saccades gain gave 1.03 ± 0.06 for ViC, 1.07 ± 0.06 for RVeC and 1.03 ± 0.15 for SVeC. Therefore, while all conditions lead to similar mean accuracy, the variability was larger in SVeC (as suggested by the lower r^2 seen
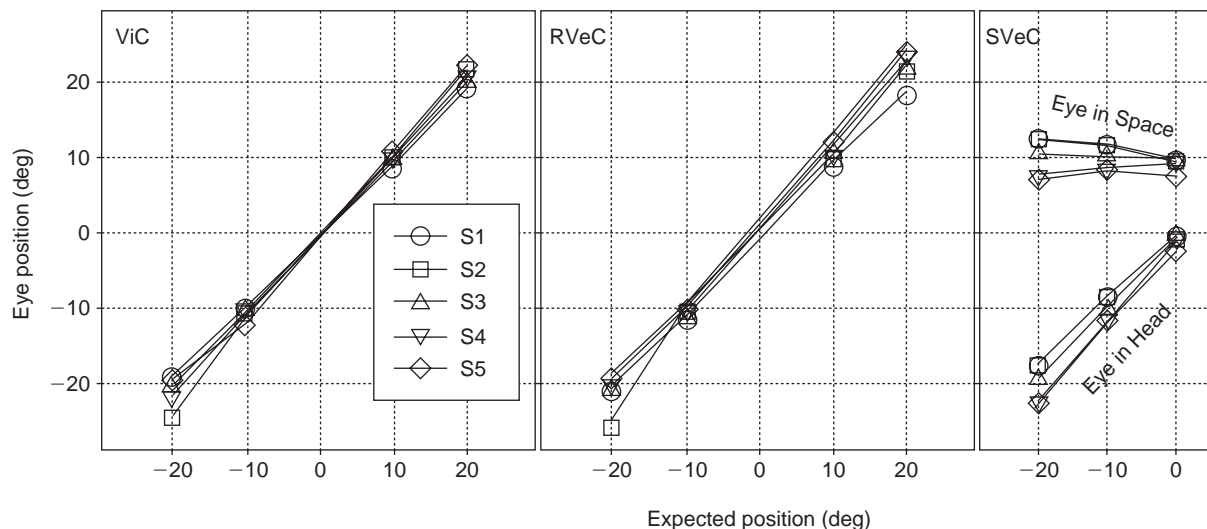

FIG. 1.   Mean measured eye position of each subject in all three conditions against expected eye position. In SVeC, both eye in head (as in both other conditions) and eye in space (E + H) positions are plotted.

above). The gain variability increased with F eccentricity in ViC , with H angle in SVeC and with both H and F in RVeC.

Error: Gain could not be computed in SVeC for chair rotation of 10°; in this situation the subjects were supposed not to move their eyes since the previously seen target F was precisely at 10°. This situation will be referred to as zero spatial error (ZSE).

When the absolute error was considered (Fig. 2), the repeated measures ANOVA for all three conditions was very significant ($F(2,4) = 8.817$, $p = 0.0095$). The *post-hoc* test revealed that ViC error ($1.77 \pm 0.49°$) was significantly different from RVeC error ($2.40 \pm 0.51°$; $p < 0.05$) and from SVeC error ($2.78 \pm 0.74°$; $p < 0.01$) while there was no difference between RVeC and SVeC errors. When we omitted the ZSE trials of SVeC, error of SVeC was then $3.20 \pm 0.73°$, i.e. larger than in the average computation including the ZSE trials (Fig. 2). Therefore, statistical analysis results were still more significant ($F(2,4) = 11.103$, $p = 0.0049$), and the difference between the error of RVeC and that of SVeC was also significant ($p < 0.05$).

Learning: As a visual target was presented in the true location as a visual feedback, the subjects could correct their eye position after each trial and some learning could be expected. Surprisingly, learning was indeed observed, but only in SVeC. The absolute error was as large as $7.51 \pm 6.13°$ at the first trial and $2.25 \pm 2.45°$ at the 30th trial, but a stable performance was reached by the fifth trial. In both other conditions the performance remained stable throughout the whole experiment (Fig. 3). Supporting this learning process, the intra-individual variability of absolute error was significantly larger ($F(2,4) = 34.312$, $p = 0.0001$) in SVeC ($2.92 \pm 0.62°$) than in both other conditions ($1.52 \pm 0.50°$ in ViC,
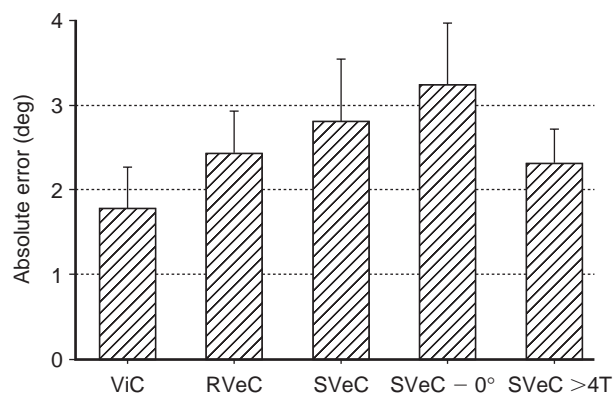

FIG. 2. Eye position absolute error (mean ± s.d.). The fourth column shows SVeC without the 0° saccade trials (ZSE), and the fifth column SVeC without the first four trials.
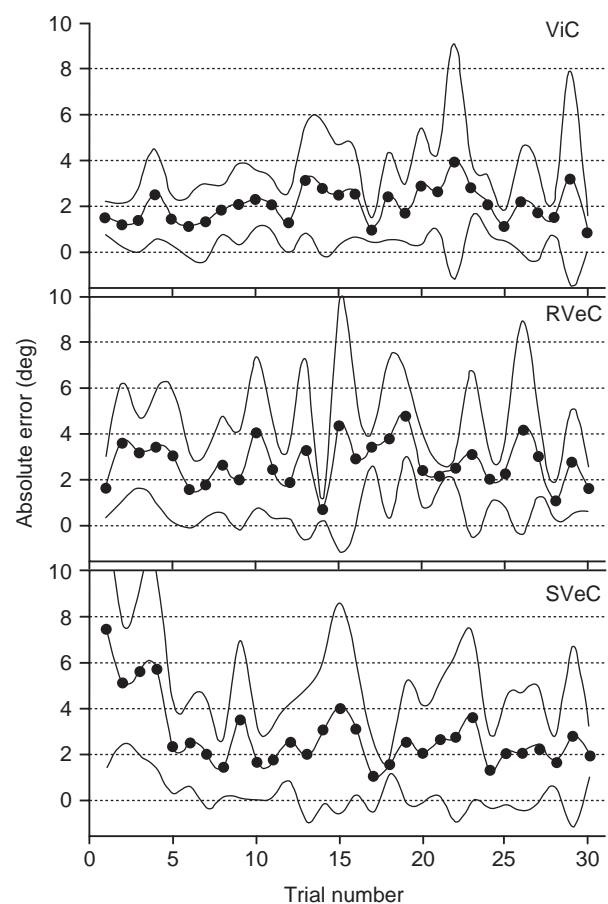

FIG. 3. Learning. Absolute eye position error of the first 30 trials for each condition.

$2.08 \pm 0.53°$ in RVeC). When we re-computed the absolute error of SVeC without the first four trials for each subject ($2.27 \pm 0.41°$) there was no significant difference between the three conditions (Fig. 2). Finally, we checked the difference in absolute error between the trials before and after the fourth one, in SVeC, for all expected responses (0, 10 and 20° saccades). This difference was much larger for the ZSE trials ($7.32 \pm 4.95°$ improvement after the fourth trial) than for the 10° ($2.77 \pm 2.05°$ improvement) and 20° expected saccade trials ($1.58 \pm 0.99°$). The difference (between the differences) was significant ($F(2,12) = 4.634$, $p = 0.032$), and according to the *post-hoc* test it was significant between 0 and 10° expected saccade trials and between 0 and 20° but not between 10 and 20°.

Discussion

In this study we investigated two aspects of vestibular multisensory integration in the context of visual space updating process: when the vestibular signals have to be ignored to maintain constant the stored visual information (RVeC), and when the vestibular

signals have to be processed to modify the stored visuo-spatial information (SVeC). The data show different mechanisms involved in these two visuo-vestibular interactions.

Maintaining the stored retinotopic information: In a task of visual memory-guided saccades, the visual signal that is the retinal error is stored and retrieved to produce accurate eye movements in space. In the condition (RVeC) of head rotation after the acquisition of visual information, we might expect some changes in saccade accuracy to the memorized visual target location compared to the condition when no sensorimotor interference is added (ViC). We suggest two possible mechanisms in the condition of vestibular interference during visual information storing (RVeC): either the central nervous system (CNS) reconstructs both target position and body rotation, or simply neglects body rotation so that it is as simple as in ViC. Interestingly, the saccades were performed with good accuracy without any learning in these two conditions. As there was no learning in RVeC, we hypothesized that there was no visuo-vestibular computation involved in this condition, and that the CNS indeed neglected body rotation. This is a special case of selection of the sensory information channels.

The absolute error in RVeC was larger than in ViC: body rotation apparently disturbed and/or interfered with the single retinotopic memory-guided saccade. This disturbance could be attributed to attentional factors, as rehearsal or imagery could have been impaired during the rotation, when the subject had to concentrate on the head-fixed target. In their study of memory-guided saccades, Gnadt et al. [16] attributed the spatial distortion of the end position to the fact that the memory of intended eye movement does not retain accurate retinotopic registration. The present results do support this interpretation.

Processing (updating) the stored visual information: In the condition when the retinal error had to be transformed to take into account the head rotation (SVeC), the gain of the ocular final position of memory-guided saccades was close to 1 and not different from the two other conditions. This result suggests that vestibular inputs are correctly integrated to visual information to reconstruct the absolute location of the target in space. At least, the visuo-vestibular computation involved in the SVeC results in a final eye position as accurate as in the two other retinotopic conditions ViC and RVeC. However, the error of the final eye position in SVeC was larger as well as the variability. This suggests that the task was more difficult as a neural computa-

tion of the visual and the vestibular signals was required. Indeed, this is supported by the learning trend, observed in SVeC only. Subjects had to add the remembered target eccentricity F to the successive head rotation angle. Although it could be argued that such behavior is rather common in everyday life, it is never performed in complete darkness, as it was during the present experiment. The fact that only four trials with feedback were required to reach a performance identical to both other conditions does support the computation process: it was not adaptation, but most probably simple calibration, as required every time we try to acquire a new skill. Finally, it should be noted that the results of the zero spatial error trials of SVeC do further confirm a correct visuo-vestibular computation: indeed, while subjects were surprised because they had been instructed to make saccades to a remembered spatial location, and in that situation they did not need any saccade to be on the correct location, the errors were smaller than when a 10 or 20° saccade was expected (Fig. 2). Therefore, although this situation added some cognitive difficulty to the task in decision making ('should I move the eyes. I feel that I am already on the right spot, but I have been told to..?'), the error when a saccade was actually executed was not large, and shows that the subjects had computed their position well.

Feedback and learning: The original version of the SVeC paradigm had actually been devised by Bloomberg et al. [10,17] and named the vestibular memory-contingent saccade task (VMCS). However, the memorized target (F) to saccade to after passive whole-body rotation was straight ahead (before body rotation) in VMCS, while it was 10° right in SVeC, providing a retinal error which was absent in VMCS. Bloomberg et al. [10] found a gain of 1.01 ± 0.12, a slope of 0.84 ± 0.04 and the intercept was close to zero since the retinal error was null. Our present results are therefore quite coherent with the former [10,18]. However, the present data do not confirm those from Blouin et al. [15]. Indeed, in SVeC with F at 18° right, they found a significant correlation between the eye saccade final position (E + H = eye in space) and H, while E + H should have been constantly 18° right. This means that their subjects could not fulfill the task. This discrepancy could be attributed to the chair velocity profile, which was bell-shaped in their experiment and step-like in the present one. However, Bloomberg et al. [10] report having performed the relevant control test, comparing both velocity profiles in the VMCS task, and did not find an effect on the performance. Therefore, the examined discrepancy should be attributed to the effect of feedback: indeed, in the

present experiment subjects corrected their saccadic response (if necessary) after each trial, when the visual target at the correct location was presented, while in the previous experiment [15] no feedback was provided. The role of feedback (i.e. learning) is further supported by the control test executed by Blouin *et al.* [15]. They did replicate the VMCS test, but without feedback, and they found a lower slope than that of Bloomberg *et al.* [10]. The authors did also discuss this effect of learning, and they argued that with their experiments they tested the actual percept of vestibular stimulation [14]. A similar discussion had been raised by Israël *et al.* [11], who suggested that responses could be changed not only by feedback but also by the presentation of a true earth-fixed target as reference before body rotation. In some experiments [11,13–15], including the present study, the initial target was the chair-fixed one, while in others [10,12] the earth-fixed target was different from the chair-fixed one. This criterion probably affects both self-motion perception and the subsequent goal-directed action. Finally, although Bloomberg *et al.* [10] claimed that the performance in the VMCS task did not vary with feedback, the rapidity of the calibration process we observed in the present experiment shows that it can escape classical statistical analysis.

Medendorp *et al.* [19] recently investigated the ability of human subjects to account for a self-initiated step when pointing to remembered targets, and found that the step biased the pointing in the same direction as the step. While their results support and extend previous studies [13–15] it should again be pointed out that no feedback was provided to the subjects during the experiment.

In conclusion, our data show that vestibular information does contribute to update the internal spatial representation of visual information when a visual feedback is provided. Does the apparent necessity of feedback cancel the genuine vestibular involvement in such computational operation? We believe not. However, as the vestibular system and the saccadic one do usually work with different coordinates systems, matching cues have to be provided in order to share the egocentric reference frame required in the present experiment. One way to validate this hypothesis could be to give feedback to only one single spatial response instead of all responses.

Conclusion

We investigated vestibular multisensory integration in the context of visual space updating process when the vestibular signals have to be ignored to maintain constant the stored visual information (RVeC) and when the vestibular signals have to be processed to modify the stored visuo-spatial information (SVeC). In RVeC, body rotation apparently disturbed and/or interfered with the retinotopic memory-guided saccade. This disturbance could be attributed to attentional factors, as rehearsal or imagery could have been impaired during the rotation, when the subject concentrated on the head-fixed target. The error in SVeC was larger, as was the variability. The task was more difficult as a neural computation of the visual and the vestibular signals was required. Indeed, this is supported by the learning trend, observed in SVeC only. The fact that only four trials with visual feedback were required to reach a performance identical to other conditions does support the idea of a visuo-vestibular computation process. Our data show that vestibular information does contribute to update the direction where to look, when a visual feedback is provided.

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