Original Contribution

VISUAL OBJECT LOCALIZATION THROUGH VESTIBULAR AND NECK INPUTS. 2: UPDATING OFF-MID-SAGITTAL-PLANE TARGET POSITIONS

Jean Blouin, Gabriel M. Gauthier, and Jean-Louis Vercher
UMR CNRS Mouvement et Perception, Faculté des sciences du sport, C.P. 910, Université de la Méditerranée, 163, Avenue de Luminy, 13009 Marseille, France
Reprint address: J. Blouin, UMR CNRS Mouvement et Perception, Faculté des sciences du sport, C.P. 910, Université de la Méditerranée, 163, Avenue de Luminy, 13009 Marseille, France.
Fax: +33-4-91-17-22-52; E-mail: blouin@laps.univ-mrs.fr

Abstract — The vestibular signal plays a significant role in sensing changes in head orientation during rotations and in determining the magnitude of the rotations, but has only minor contributions in updating the internal representation of object positions with respect to the body after body rotations. The small contribution of the vestibular signal in egocentric object localization was evidenced in experiments in which the subjects reported the remembered position of eccentric earth-fixed targets after passive body rotations. The experiment reported here tested whether motor systems, such as the oculomotor system, make use of vestibular signals to generate accurate goal-directed motor responses toward a target whose position needs to be updated with respect to the body during and after whole-body rotations. The results showed that although subjects can produce saccadic eye movements of about the same magnitude as passive whole-body rotations (as previously reported by a number of researchers), they failed to generate accurate saccades toward the position of an extinguished peripheral visual target after the rotation. Overall, these results combined with those found in the literature suggest different central processes for determining changes in body orientation in complete darkness and for updating a target position with respect to the body during and after body rotations. © 1997 Elsevier Science Inc.

Keywords — vestibular signal; body orientation; space perception; object localization; human.

Introduction

The function of the vestibular apparatus has been extensively studied over the last two centuries by anatomists, physiologists, psychologists, clinicians, and animal behaviorists [reviewed by Jeannerod (1), Henn and colleagues (2)]. First seen as an auditory accessory, the vestibular apparatus (that is the semicircular canals and the otoliths) became known as the equilibrium organ in the early 19th century. This function was attributed to the labyrinthine apparatus after the systematic loss of equilibrium of animals following section of the vestibular nerve. More contemporary investigations of the labyrinthine function have convincingly showed the large contribution of the vestibular signals in various motor activities (for example, vestibulo-ocular reflex, control of posture and locomotion) and also more cognitive oriented processes (for example, sensing head rotation, animal and human navigation).

Coding Body Rotation Magnitude through Vestibular Signal

A considerable number of experiments have been devoted to the study of the central nervous system’s (CNS) capacity to process vestibular signals to determine head (or body) orientation
following rotations [for example, (3–9)]. Generally, an individual passively rotated about the vertical axis in the dark can determine fairly accurately the magnitude of the rotation. This implies that the output from the (horizontal) semicircular canals (which respond to acceleration) can be integrated over time to give a position signal. Thus, the CNS is equipped with integrators [one "mechanical-type" within the vestibular apparatus itself and another neuronal, see reference (10)] that allow one to determine the magnitude of passive whole-body rotations without input signals from the environment, which could be transmitted through vision, for instance. Therefore, sensing a change in body orientation after a rotation and determining the rotation magnitude can both be considered as being purely interoceptive tasks.

**Calibration of the Vestibular System at the Perceptual Level**

Vestibular and body proprioceptive signals (mainly originating from neck muscles) converge at several areas of the CNS. For instance, individual cells of the vestibular nucleus (11–13), thalamus (14), and parietal cortex (15,16) have been found to respond to both proprioceptive and vestibular inputs. The integration of vestibular input and neck proprioception (subtraction of the two inputs) is known to be essential for determining motion of the trunk in space, as described by Maurer and his colleagues in the accompanying article (17).

Another hypothetical function for this massive convergence of these two signals is that perception of body orientation requires the integration of both vestibular and neck–body proprioceptive signals (14). This hypothesis has recently received support from an experiment studying the perception of body rotations in a patient without proprioception of the neck and body muscles (18). The results showed that, in the absence of neck and body proprioception, the perception of passive body rotations in darkness is largely impaired, despite normal gaze stabilization during head rotation through the vestibulo-ocular reflex (VOR). The deafferented patient constantly overestimated the magnitude of the body rotations both when reproducing rotation magnitude through a saccade in the opposite direction to the rotation and when reporting verbally the magnitude of the rotations.

Such large overestimation of body rotation magnitude (the return saccade of the patient often reached twice the rotation magnitude) despite normal VOR suggests that the absence of neck muscle proprioception may cause an improper calibration at the perceptual level of the vestibular apparatus necessary for determining the magnitude of passive whole-body rotations. Indeed, neck proprioception is a good candidate for calibrating vestibular inputs for normal subjects because it is the only signal that constantly provides reliable information about changes in head-to-trunk position during and after head rotations (8,19,20).

**Coding Stationary Object Positions with Respect to the Body during Head Rotations**

The fact that the brain can process vestibular signals during passive body rotations to determine the magnitude of the rotations does not necessarily imply that the vestibular signal is also used to update the position of objects with respect to the body (head) during or after rotations. Localizing the new object position with respect to the body after rotations requires not only a good capacity for coding body rotation magnitude through vestibular input, but it also necessitates access to the vestibular signal by the systems specialized in the object localization function.

Recently, we have investigated the capacity of the CNS to process the vestibular signal not in interoceptive tasks such as those testing perception of passive body rotation signal not in the dark, but in a task requiring an interaction between a stimulus presented in the environment and the body (4). In one series of experiments, a visual target was briefly presented in the peripheral visual field (18°) before rotating the subject while he maintained gaze at a chair-fixed target to cancel the VOR. After the rotation, the subject judged the new position of the extinguished visual target with respect to the
Spatial Processing during Body Rotations

body (that is, target to the right or to the left of the body midline, which was represented by the chair-fixed target, or aligned with it). A good capacity for judging the position of remembered visual targets with respect to the body after passive whole-body rotations might have suggested that the vestibular signal was involved in the processes updating the internal representation of the visual space during head movements and that the vestibular signal may be incorporated in a feedback loop controlling spatially goal-directed head movements. However, results showed great inaccuracy in determining body orientation with respect to the extinguished visual target. The subjects had to be rotated nearly twice the magnitude of the visual target to perceive the flashed target aligned with the body after the rotation.

We have considered the possibility that these findings could have resulted from the poor spatial resolution characterized by the subject's response. For instance, the subjects may have reported that they were not aligned with the extinguished visual target when they perceived they were just a few minutes of arc from the target after the rotations. Therefore, the methods used may have magnified errors in true body-target relative position perception. We tested this possibility by asking subjects to direct a laser beam after the rotation to the position where they perceived the target was presented before the rotations (5). This method allowed us to extract the actual perceived position of the previously presented target. Again, the subjects largely underestimated their body orientation with respect to the memorized visual target position. On average, the subjects integrated only 60% of the whole-body rotation when determining the egocentric position of the visual target presented before the rotation. These findings suggest that, alone, the vestibular signal cannot yield accurate updating of the internal representation of object positions with respect to the body during and after rotations.

Use of the Vestibular Signal by Perceptual and Motor Systems

The results presented above showed that the perceptual systems cannot count, at least exclusively, on the vestibular signal to accurately determine the egocentric target position during head rotations. However, there is a possibility that the sensorimotor systems can make use of vestibular signal to generate accurate goal-directed motor responses toward a target whose position has to be updated with respect to the body during and after head rotations. Experiments showing that motor systems may have access to spatial information that may not be available to the perceptual systems are in line with such a hypothesis [for example, (21–25)]. Moreover, some motor systems such as the oculomotor system have very tight relationships with the vestibular apparatus [see, for instance, reference (26)]. The close links between the vestibular and the ocular systems could indeed explain the fairly good accuracy found by several authors when subjects reproduced perceived passive whole-body rotation magnitudes with saccades in the opposite direction to the rotation (3,7). Similar accuracy when generating saccades toward the remembered position of an eccentric target and when generating saccades to reproduce the rotation magnitude may suggest that these two tasks share similar processes and that they may interrogate the same systems. The experiment reported below was designed to test this possibility.

Materials and Methods

Subjects

Four subjects participated in this experiment on a voluntary basis. Their age ranged from 25 to 43. Each subject provided informed consent to participate in this study.

Apparatus and Procedure

The apparatus used in this experiment is schematically presented in Figure 1. The subjects sat in a completely dark room on a chair positioned at the center of a black cylinder. The subject could be manually rotated around the vertical axis using the handle attached at the rear of the platform supporting the chair. A bell-
shaped velocity profile was used to rotate the subject because it simulates the velocity profiles of natural active head movements (27,28). The head of the subject was immobilized with respect to the trunk using a bite-bar, and eye movements were minimized during rotations by the fixation of a chair-fixed target (CFT) positioned straight-ahead. Chair rotations and eye movements were measured using a potentiometer and electro-oculography, respectively. All signals were digitized at 100 Hz.

In the no-target condition, after the rotation, the subject produced a saccadic eye movement to shift gaze to the position fixed before the rotation ("vestibular memory-contingent saccades" paradigm, proposed by Bloomberg and colleagues (29)). No feedback about accuracy was provided after the saccade. Therefore, in this task, the subject had to process and to memorize the vestibular signal elicited during the rotation to produce a saccade of equal magnitude but in the opposite direction to the passive whole-body rotation. The rotation magnitudes, pseudo-randomly selected, were either 6°, 12°, 18°, 24°, 30°, or 36° rightward.

In the target condition, a visual target (light-emitting diode) was presented for one second at 18° at eye level to the right of the subject’s midline while he was fixating the CFT. The subject was instructed to not foveate the peripheral target and to maintain gaze toward the CFT. After target extinction, the subject was rotated in the target direction. The magnitude of the rotations were similar to those of the no-target condition and were then either smaller, equal to, or greater than the visual target amplitude. After the rotation, the subject produced a saccade to shift gaze to the position of the previously presented visual target. Therefore, in this task, the output of the vestibular apparatus had to be processed by the systems specialized in the visual function to update the internal representation of the target position with respect to the body after the rotations.

Results

Representative results from one subject in the no-target condition are presented in Figure 2A, where the magnitudes of the saccadic eye movements are plotted against the rotation magnitudes. Results obtained in the target condition by the same subject are presented in Figure 2B, where gaze directions after the saccades are plotted against rotation magnitudes. First, linear regression analyses were used to evaluate saccadic eye movement accuracy in both conditions. Perfectly accurate movements would be characterized by a slope of 1 with an intercept of 0 in the no-target condition, whereas these linear regression parameters would be equal to 0 (slope, that is, final gaze direction does not vary with body rotation magnitude) and 18 (intercept, that is, target position) in the target condition. Positive and negative slopes for the latter condition would suggest respectively low and high gains of the vestibular information for updating a target position during head rotations. Table 1 provides the regression parameters measured for each subject.

High $r^2$ values were found for all subjects and conditions. The subjects tended to slightly underestimate the magnitude of the passive whole-body rotation, as evidenced by positive slope values below unity (ranging from 0.73 and 0.84 between subjects, mean of 0.79). The magnitude of the underestimation when deter-
mining the magnitude of body rotations corroborates the magnitude previously reported in the literature (for example, 4,5,7). Of particular importance is the high correlation between the rotation magnitude and the perceived position of the stationary 18° visual target. This result suggests inaccuracy in updating the egocentric position of the target during passive whole-body rotations. The slope values of the regression lines in the target condition ranged between 0.44 and 0.55 and had a mean of 0.50. These relatively high positive slope values show that subjects underestimated rotations when comparing body orientation with an earth-fixed target. This underestimation, which is similar to that found in more perceptually oriented tasks [for example, (4,5)], is markedly greater than that found in the no-target condition, in which subjects had only to determine rotation magnitudes, with no relation to a visual target position.

Figure 3 presents the errors (averaged between subjects) in the processing of the vestibular signal for each condition and rotation magnitude. These errors were calculated in relation to rotation magnitude in the no-target condition and in relation to target eccentricity in the target condition. Positive and negative values indicate overestimation and underestimation of the rotation, respectively. The errors were submitted to a 2 × 6 [Condition (no target, target) × Magnitude (6°, 12°, 18°, 24°, 30°, 36°)] analysis of variance (ANOVA). The ANOVA revealed significant main effects of Condition ($F[1, 3] = 69.28, P < 0.0001$) and Magnitude ($F[5, 15] = 108.03, P < 0.0001$) conditions. The ANOVA also showed a significant interaction Condition × Magnitude ($F[5, 15] = 18.82, P < 0.0001$). For rotation magnitudes superior to 12°, the error in the vestibular signal processing was greater.

Table 1. Linear Regression Parameters Representing the Perceived Rotation Magnitudes (No-Target Condition) and the Perceived Position of the 18° Flashed Visual Target after Rotations (Target Condition)

<table>
<thead>
<tr>
<th>Subject</th>
<th>No-Target</th>
<th></th>
<th>Target</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>Intercept</td>
<td>$r^2$</td>
<td>Slope</td>
<td>Intercept</td>
<td>$r^2$</td>
</tr>
<tr>
<td>1</td>
<td>0.82</td>
<td>0.01</td>
<td>0.92</td>
<td>0.52</td>
<td>11.67</td>
<td>0.92</td>
</tr>
<tr>
<td>2</td>
<td>0.73</td>
<td>1.73</td>
<td>0.95</td>
<td>0.44</td>
<td>16.66</td>
<td>0.81</td>
</tr>
<tr>
<td>3</td>
<td>0.76</td>
<td>-0.81</td>
<td>0.94</td>
<td>0.48</td>
<td>16.33</td>
<td>0.89</td>
</tr>
<tr>
<td>4</td>
<td>0.84</td>
<td>0.40</td>
<td>0.92</td>
<td>0.55</td>
<td>12.03</td>
<td>0.89</td>
</tr>
</tbody>
</table>
when subjects determined the position of the memorized earth-fixed target after the rotations than when the task required only body rotation magnitude determination. On the other hand, these errors increased with rotation magnitude.

Discussion

Previous studies have shown a good capacity of the CNS to process labyrinthine signals during passive whole-body rotations and translations to retrieve position of the body before the displacement, though an underestimation of about 15% to 20% is generally found when no feedback about accuracy is given to the subjects (3, 7, 29–33). These findings suggest that signals from the labyrinthine apparatus provide reliable information for determining the direction and the magnitude of body displacements.

We have shown in recent studies (4,5) that the vestibular signals elicited during passive whole-body rotations cannot be used by the perceptual systems to accurately determine the egocentric position of a flashed visual target after passive whole-body rotations. The results from the present experiment generalize these findings to the oculomotor system: the subjects failed to produce accurate saccades to an earth-fixed target after body rotations. As highlighted in Figures 2 and 3, the subjects markedly underestimated the rotation magnitudes when shifting gaze to the target presented before the rotation. For rotations greater than 12°, the subjects underestimated the rotations by about 36% (compared to 20% when subjects produced saccades to the starting position).

Overall, these results combined with those discussed in the introduction suggest different central processes for determining changes of body orientation in complete darkness and for updating a target position with respect to the body during and after body rotations. In the former, good approximation of body rotation magnitude is obtained through integration of the vestibular signal over time during the rotations. In the latter, the vestibular signal has not only to be integrated over time, but it must reach and be processed by the systems specialized in the visual object localization function to keep track of the target position with respect to the body during the rotations. According to this framework, determining passive rotation magnitude may be considered as being a purely interoceptive task, whereas coding object position after a rotation requires integration of signals from the environment and signals about body motion and can therefore be considered as an egocentric task.

Natural gaze shifts, either toward a visual target or away from it, are usually accomplished through a combination of eye and head movements providing the CNS not only with vestibular information to update the target position with respect to the body, but also with retinal and extraretinal signals, neck muscles proprioceptive information, and also the efference copy of motor commands producing head movements. The weight of these various sources of information in updating the egocentric object position during movements is likely task dependent and also a function of the strategy used by the observer to solve the spatial problem [see (8, 34–37)].

Acknowledgments—This study received financial support from Human Frontier Science Program (no. RG-58/92). The authors wish to thank Andrea Griffin for helping to improve the style of the English.
REFERENCES