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Updating visual space during passive and voluntary head-in-space movements

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Abstract The accuracy of our spatially oriented behaviors largely depends on the precision of monitoring the change in body position with respect to space during self-motion. We investigated observers' capacity to determine, before and after head rotations about the yaw axis, the position of a memorized earth-fixed visual target positioned 21° laterally. The subjects (*n*=6) showed small errors (mean=–0.6°) and little variability (mean=0.9°) in determining the position of an extinguished visual-target position when the head (and gaze) remained in a straight-ahead position. This accuracy was preserved when subjects voluntary rotated the head by various magnitudes in the direction of the memorized visual target (head rotations ranged between 5° and 60°). However, when the chair on which the subjects were seated was unexpectedly rotated about the yaw axis in the direction of the target (chair rotations ranged between 6° and 36°) during the head-on-trunk rotations, the performance was markedly decreased, both in terms of spatial precision (mean error=5.6°) and variability (mean=5.7°). A control experiment showed that the prior knowledge of chair rotation occurrence had no effect on the perceived target position after head-trunk movements. Updating an earth-fixed target position during head-on-trunk rotations could be achieved through both cervical and vestibular signals processing, but, in the present experiment, the vestibular output was the only signal that had the potentiality to contribute to accurate coding of the target position after simultaneous head and trunk movements. Our results therefore suggest that the vestibular output is a noisy signal for the central nervous signal to update the visual space during head-in-space motion.

Key words Spatial orientation · Head-neck system · Vestibular · Head movement · Human

Introduction

Spatial processing allows individuals to have a sense of where they are in an environment and to determine the position of elements of this environment with respect to their body. Spatial processing is therefore involved in many motor and perceptual activities, such as goal-directed walking, object grasping, or gaze shifting towards peripheral objects. One approach to the study of spatial vision consists in acquiring knowledge about how the hypothetical internal representation of space is built. For instance, researchers have investigated the role of visual experience in constructing a mental representation of space (Loomis et al. 1993; Thinus-Blanc and Gaunet 1997; Warren and Pick 1970) or tested the effect that different types of exploration (e.g., passive versus active exploration) have on the accuracy of spatial navigation (Péruch et al. 1995). Another approach consists in studying the mechanisms by which this central representation of space is updated during self-motion. One of the goals of these studies is to gain insights into the signals (retinal and non-retinal) processed by the central nervous system (CNS) in determining the position of an object with respect to the body before, during, and after eye, head, or body movements (Blouin et al. 1997a; Glasauer et al. 1994; Loomis et al. 1992).

The present experiment investigated the possibility of healthy human subjects to process vestibular signals to determine the position of visual objects before and after head-in-space motion. The contribution of the labyrinths to spatial behavior has been extensively studied over the years (for reviews, see Cohen et al. 1992; Howard 1982). It has been shown that subjects perceive with relatively good accuracy the magnitude of whole-body rotations about the yaw axis in darkness (Bloomberg et al. 1988; Blouin et al. 1995c; Guedry et al. 1971; Israël 1992; Israël et al. 1993; Maurer et al. 1997; Mergner et

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al. 1991). Because the semi-circular canals respond to angular acceleration, a double integration is needed to estimate body orientation after passive rotations. A first peripheral integration is carried out within the vestibular apparatus itself and the second is carried out in the CNS (McFarland and Fuchs 1992; Robinson 1989).

Despite the relatively good accuracy in determining the amplitude of whole-body rotations in the dark, the contribution of vestibular output to the process of updating visual space during self-motion has yet to be demonstrated. Indeed, the perception of memorized peripheral earth-fixed target positions after passive whole-body rotations about the yaw axis is largely inaccurate (Blouin et al. 1995a,b, 1997, 1998, in press). The inaccuracy in updating visual space through vestibular signals processing has been found with different experimental protocols requiring healthy subjects either (1) to verbally estimate the memorized target position with respect to body midline after whole-body rotations (e.g., the extinguished visual target is to the right of the body midline), (2) to displace a visual source to the position of the extinguished visual target after the rotations, (3) to point with the finger, or (4) to produce a saccadic eye movement in the direction of the memorized visual target after the rotations.

Common to these studies is the fact that the labyrinthine apparatus was stimulated passively with respect to the subject by rotating the chair on which the observer was seated. However, it is possible that vestibular signals make a limited contribution in updating space when head rotations in the dark are not self-generated or when the vestibular output is not associated with changes in neck-muscle proprioception and efference copies. This issue was investigated in the present experiments, in which head-in-space position was changed through either voluntary head-on-trunk rotations or a combination of both voluntary head movements and passive trunk rotations about the yaw axis.

Experiments using combined head and trunk rotations have already been carried out by other authors to respond to related questions (e.g., Maurer et al. 1997; Mergner et al. 1983, 1991). For instance, Maurer and colleagues (1997) tested whether subjects can determine either the head-trunk relative position or the magnitude of the head displacement after passive head and trunk rotations about the yaw axis. To this end, the subjects were asked to position a visual source in front of either the head or the trunk midline after a combination of passive head and trunk movements or to indicate the perceived magnitude of the head-in-space motion by displacing a visual source to the position that corresponded to straight-ahead before the rotations. They found that subjects were able to accurately determine the positions of the head and the trunk after such rotations, whereas the straight-ahead position tended to be misjudged in the trunk's direction.

However, it is not certain whether the precision of a subject in perceiving the magnitude of the head-in-space displacement can predict his ability to determine either head or body positions with respect to objects in the environment following simultaneous head and trunk movements. Indeed, it is conceivable that a subject may be able to determine the absolute amount of passive head displacement without being able to refer his head (or body) position to the environment after such rotations. This could be possible because the magnitude of the head-in-space displacement can be approximated by processing vestibular output without the presence of reference cues from the environment (auditive or visual, for instance). To retrieve the position that corresponded to straight-ahead before the rotations, observers can therefore reproduce, in the opposite direction, the magnitude of the head movement. Hence, we cannot exclude the possibility that the accuracy with which the subjects indicated the straight-ahead position after head-trunk rotations in Maurer and colleagues' (1997) study may rely more on the capacity of the CNS to process the vestibular output to approximate the extent of head-in-space motion in the dark than on its capacity to actually update visual space through vestibular output during body motion. This hypothesis is supported by several recent studies showing that, after passive whole-body rotations, subjects can determine the magnitude of the rotations with good precision, but are markedly inaccurate when they have to judge the position of a visual target initially presented in the peripheral visual space (Blouin et al. 1995a,b, 1997, 1998, in press). For this reason, in the present experiment, we asked the subjects to indicate, after head or head/trunk motions, the position of a visual target previously presented in the periphery.

Materials and methods

Subjects

Six healthy right-handed volunteers participated in the study. Their ages ranged from 23 to 39 years (mean age: 27.8 years). All subjects gave informed consent to participate in the study and the local ethic committee accepted the experimental protocol.

Apparatus and procedure

A schematic representation of the apparatus is shown in Fig. 1. The observer sat on a revolving chair with his arms on the armrests. The chair was positioned at the center of a semi-circular black cylinder with a radius of 1 m. The chair could be passively rotated about the vertical axis by hand by the experimenter. An array of light-emitting diodes (LED), placed behind the chair, served to indicate to the experimenter the magnitude of the chair rotations to be produced when required. Chair angular excursion was measured with a potentiometer fixed at the center of rotation of the chair. Chair motions had a bell-shaped velocity profile. Head-on-trunk rotations were measured with a potentiometer fixed on a helmet wore by the observer. More details about chair- and head-rotation velocity are presented in Fig. 2. All signals were sampled at 100 Hz through a 12-bit analog/digital converter. Hearing was masked with white noise played through headphones.

A LED was positioned straight-ahead ('central light') and a second at 21° ('target') to the right of the observer at eye level on the inner wall of the cylinder. Another LED was fixed to the tip of an 80-cm rigid light rod attached to the front of the helmet. Observers were instructed to gaze at this straight-ahead head-fixed light (HFL) throughout the trials. The experiments were carried out in a completely dark room.

Subjects used a laser diode to indicate the perceived position of the extinguished 21° target after head-trunk rotations (see 'Experimental conditions'). The laser was mounted on the vertical axis of a motor that could be activated with a joystick fixed on the right armrest. The subjects could move the laser beam along a horizontal path, 5 cm above the target level with either a high velocity (12°/s) for large displacements or with a low velocity (6°/s) for small adjustments in final laser position.

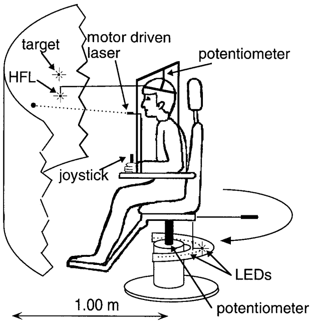

Fig. 1 Schematic representation of the apparatus used in the experiment. *HFL* Head-fixed light. See the text for the details

Experimental conditions

Figure 3 shows typical raw recordings for one subject in all tested conditions.

Head rotations (HR)

At the start of a trial, the HFL and the central light were both illuminated. The subjects were instructed to gaze at the HFL and to align the head with the central light. After 2.5 s, the 21° target was turned on for 1.5 s, after which the central light was turned off and subjects rotated the head in the same direction as the target, but with different magnitudes. The subjects self-selected the size of the rotations and were instructed to cover a 5° to 60° range of rotations. Subjects gazed at the HFL during head motions to minimize ocular movements (vestibulo-ocular reflex cancellation). After the head rotations, the laser was turned on and the subjects attempted to position it, using the joystick, on the target position while maintaining fixation on the HFL and the achieved head-angular position.

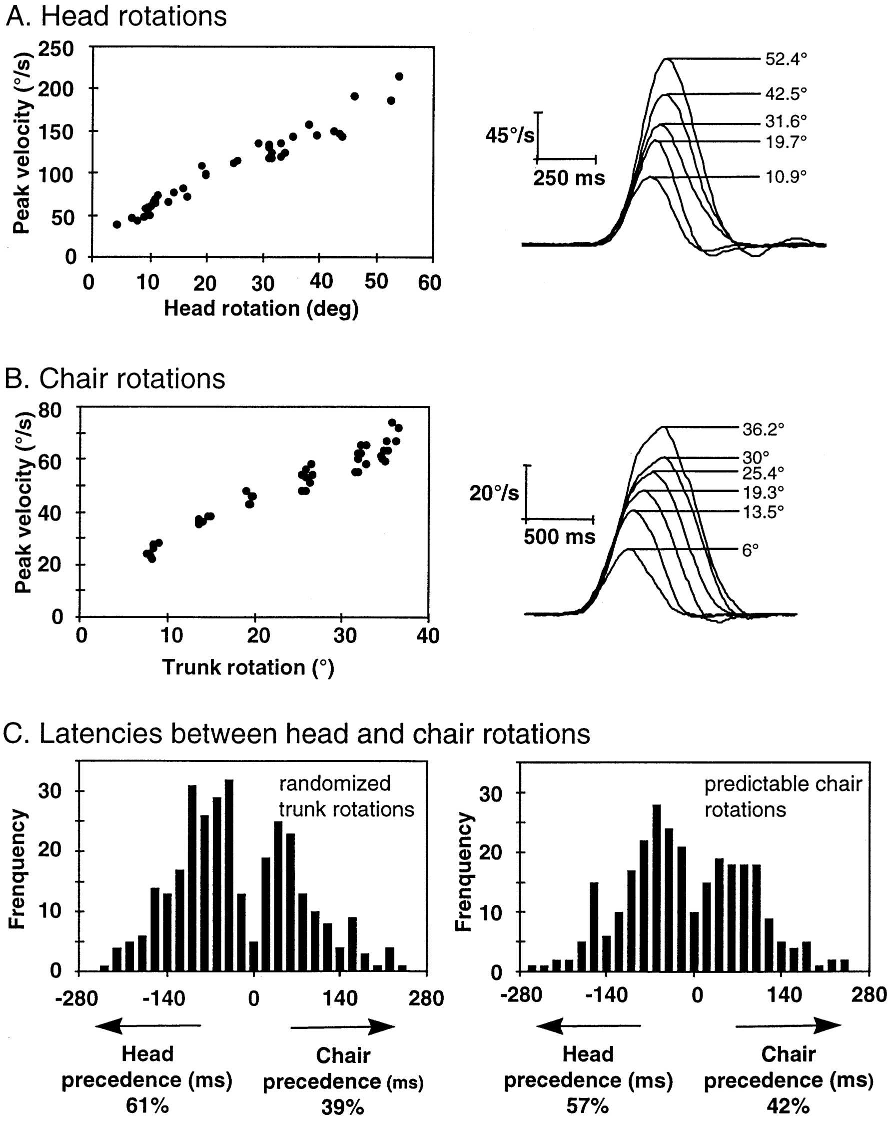

Fig. 2 Peak velocities and velocity profiles for different head- (**A**) and chair- (**B**) rotation magnitudes. **C** Frequency histograms of latencies between head and chair rotations from all subjects in the experiment where they were not aware of whether or not they would be submitted to whole-body rotations (*left panel*) and in the control experiment where chair rotations occurred in every trial (*right panel*). Bin length=20 ms

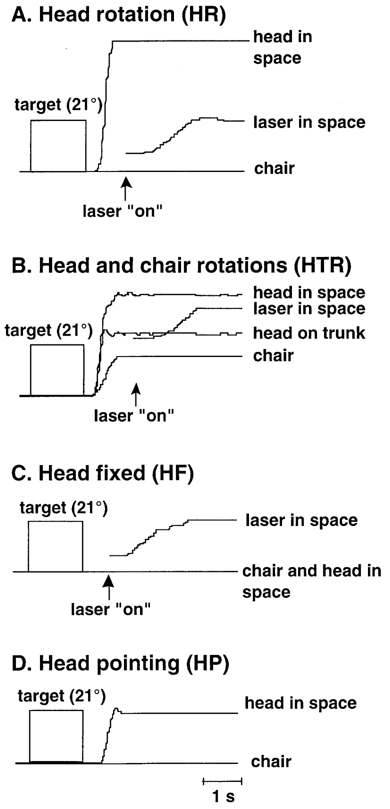

Fig. 3A–D Examples of raw recordings from each experimental condition

After the trial, the laser was turned off and the subjects moved it to a new (unknown) position by pushing the joystick back and forth. We deliberately used only one peripheral target in order to minimize the errors attributed to encoding of the target position before the rotations, which could be accrued with the use of several targets [e.g., range effects (Jeannerod 1988; Poulton 1980)]. Forty trials were performed in this condition.

Head and trunk rotations (HTR)

In some trials (n=40), the chair on which the subjects were seated was rotated about the yaw axis in the same direction as that of the target during head rotations. The magnitude of the chair rotations, selected pseudo-randomly by computer, varied between 6° and 36°. Trials with and without chair rotations were randomized in their presentation (with the two other experimental conditions presented below), and the subjects were not informed if they would be submitted to whole-body rotations. We chose to rotate the chair by hand rather than using a motor, because the latter method produces noise and vibration that could provide information to the subject about occurrence and duration of the chair rotations. Temporal coupling between head and chair rotations was assured by the fact that the LED behind the chair, which indicated to the manipulator both the timing and the magnitude of the chair rotations to be produced, was lit simultaneously with the extinction of the 21° target, which indicated to the subjects the time for initiating the voluntary head movements. However, because reaction times for initiating head and chair rotations were rarely exactly the same and because small head movements sometimes occurred during large chair rotations (and vice versa), only sections of the head and chair rotations occurred simultaneously. Therefore, with this condition, cervical (i.e., proprioception and efference copy) and vestibular signals provided different information about head-in-space rotation. Figure 2C shows a frequency histogram of latencies between head and chair rotations from all subjects. The voluntary head movements started prior to the chair rotation in 61% of the trials. Trials with non-simultaneous head and chair rotations were discarded during off-line analysis.

Head fixed (HF)

We also tested the subjects' perception of the memorized target position without any previous head and trunk rotations. In these trials (n=8), the subjects were instructed to keep the head (and gaze) in the central position throughout the trial and to direct the laser towards the extinguished target position when the laser was turned on.

Head pointing (HP)

Finally, in a control condition, we tested the subjects' accuracy in producing goal-directed head movements towards the remembered target position. Here, in eight trials, the subjects were asked to produce a movement of the head towards the memorized visual target position.

Results

We first compared the magnitude of the voluntary head movements in HR and HTR along with the total head-in-space displacement in HTR. Head-on-trunk rotations were similar whether or not the subjects were submitted to whole-body rotations (mean=21.38°), but were smaller than the extent of head-in-space displacement in HTR (mean=42.95°) [$F(2,15)=127.33$, $P<0.001$]. Moreover, the standard deviations of the means were similarly large in these variables (global mean=14.4°), denoting a wide range in the voluntary head-rotation magnitudes, as specified in the instructions to the subjects [$F(2,15)=0.88$, $P>0.05$].

For each subject, the mean final laser position in space ('perceived target position') was calculated in HF, HR, and HTR along with the mean final head position in HP. To verify whether the subjects took the passive whole-body rotations into account in their estimates of the extinguished target position in HTR, we also measured the mean final laser position with respect to the trunk. The position of the laser with respect to the trunk in both HTR and in HR should be similar if the passive component of the head-in-space motion is not taken into account in updating the position of the extinguished visual target. Variability in all these measures (i.e., standard deviation of each subject's mean) was also calculated to obtain an estimate of the reliability of the performance.

Figure 4 shows representative examples of the perceived target position for all conditions, and Fig. 5 presents across-subjects mean perceived target position and variability. The analysis of variance (ANOVA) revealed that the different experimental conditions had a significant effect on the perceived target position [$F(4, 25)=12.72$, $P<0.001$]. Planned comparison showed that the mean laser-to-trunk position was smaller in HTR than the perceived target-in-space position in the other conditions (Tukey test, $P<0.05$). There was a non-negligible tendency to overestimate the target-in-space position in

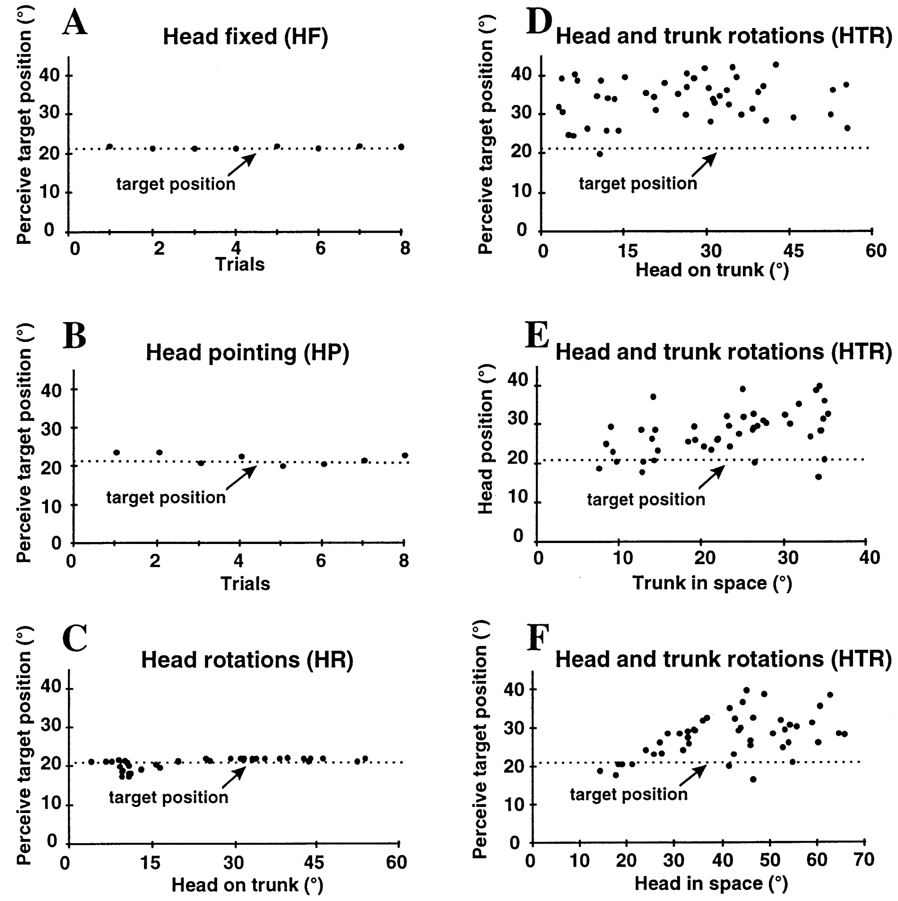

Fig. 4 A–F Performance of one subject in the different experimental conditions. For the head- and trunk-rotation (*HTR*) condition, the perceived target position is plotted against the head-on-trunk rotation magnitudes (**D**), against the trunk-in-space rotation magnitudes (**E**), and against the head-in-space displacements (**F**)

HTR (mean=26.6°) compared with the other conditions (global mean=20.8 for HF, HP, and HR), but this difference was not statistically significant.

A significant effect of the experimental conditions was also found on the perceived target-position variability [$F(4, 25)=30.77$, $P<0.001$]. The variability in the perceived target position was smaller in the conditions without trunk rotation (global mean=1.4° in HF, HP, and HR) than in the condition with combined head-trunk rotations (mean=5.7 in HTR). The variability in the laser-to-trunk position was also larger (mean=7.8°) than the variability in the perceived target position in space.

As discussed above and as illustrated in Fig. 2B, the onset of the voluntary head movements and of the trunk rotations in HTR were rarely exactly synchronized. Nevertheless, the perceived target position was similar whether the onset of head movements occurred prior to the onset of trunk rotations (mean=24.99°) or after (mean=25.50°) in HTR. The variability in the perception of the target position was also similar whether the onset of head movements occurred prior to that of trunk rotations (mean=5.89°) or after (mean=6.52°).

Linear regression analyses were used to determine for each subject whether the perceived target-in-space position was a function of either the head- or the trunk-rotation magnitudes in HTR. The equations were characterized by low r^2 values, indicating that the perceived target-in-space position was neither a function of the head-rotation magnitudes (r^2 varied from 0.01 to 0.53, mean between subjects mean=0.15) nor a function the magnitude of the chair-rotation magnitudes (r^2 varied from 0.02 to 0.63, mean between subjects=0.29).

However, the perceived target position could have been a function of the magnitude of either the head or the trunk rotations when the onset of head rotation occured either before or after the start of trunk rotation. Linear regression analyses were carried out to verify these different possibilities, and the results showed that this was not the case. Indeed, the different equations were characterized by low r^2 values. The highest mean-between-subjects r^2 value was 0.38 and was related to the equation of the linear regression obtained when the perceived target position was plotted against the magnitude of the trunk rotations when the onset of head motion occurred prior to that of trunk rotation.

Similarly, a linear regression analysis was carried out to test whether the extent of head-in-space displacements in HTR affected the perception of the target-in-space position. As shown above, head-in-space displacements were larger in this condition than in HR and could therefore account for the larger variability observed in the former condition. Again, low r^2 values were found in all subjects (r^2 varied from 0.03 to 0.43, mean between subjects mean=0.26), suggesting no significant effects of the mag-

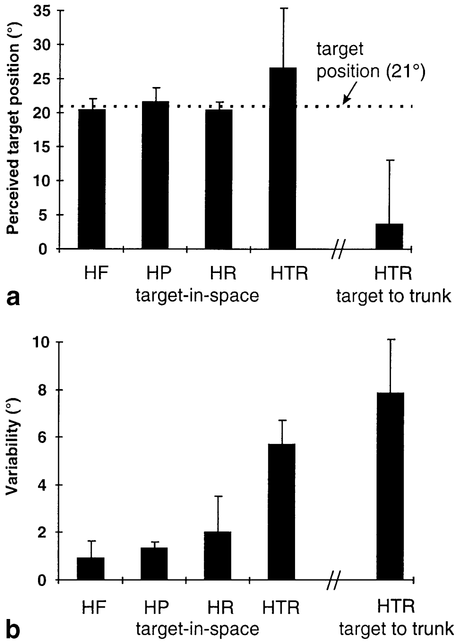

Fig. 5 Across-subjects mean perceived target-in-space position (**A**) and variability (**B**) in head fixed (*HF*), head pointing (*HP*), head rotation (*HR*), and head-and-trunk rotation (*HTR*). HTR target-to-trunk represents the mean perceived target position and variability with respect to the trunk position

nitude of head-in-space motion on the perceived target position after head and chair rotations.

We also tested whether the variability in the subjects' perception of the target position was a function of the magnitude of the head-in-space displacement in HTR. To do so, we calculated and compared the variability in the subjects' performance for head-in-space motion smaller than 40°, between 40° and 60°, and greater than 60°. The ANOVA showed no significant differences between the variability obtained in these different head-in-space motion magnitudes [$F(2, 15)=0.33$, $P>0.05$].

Results from the above experiment suggest that vestibular signals cannot be processed on-line to determine with precision the position of a memorized visual target after unexpected body rotations. As they did not know when they would be submitted to whole-body rotations, it is possible that the subjects adopted a strategy that did not take these rotations into account. In a control experiment, we tested whether the same subjects were able to determine accurately the position of an earth-fixed target after expected passive chair rotations during the voluntary head movements. In this experiment, rather than being presented randomly in a single session, the trials with and without trunk rotations (40 trials for each condition) were realized in separate testing sessions. As a consequence, the subjects knew in advance whether or not they would be submitted to passive trunk rotations during their voluntary head motion. As shown in Fig. 2C, head-movement onsets occurred prior to that of the chair rotation in 57% of the trials, which is a proportion similar to that found in the randomized trunk rotation condition.

t-tests showed no significant effects on the mean perceived target-in-space position perception ($P>0.05$) despite a tendency of the subjects to overestimate the target position in HTR, but not in HR (27.2° vs. 21.4°), as in the main experiment with the unexpected trunk rotations. Again, the subjects' perception of the target position was more variable in HTR than in HF (5.61° vs. 1.71°, $P<0.001$). This variability was significantly smaller in HTR for head-in-space displacements smaller than 40° (mean=4.72°) than for those that were greater (global mean=6.06°) [$F(2, 15)=6.77$, $P<0.01$].

As in the main experiment, the perceived target-in-space position in HTR was similar whether the onset of the voluntary head movements occurred prior to the onset of the trunk rotations (mean=27.51°) or after (mean=29.17°). The variability in the perception of the target position was also similar whether the head movements occurred prior to the trunk rotations or after (6.39° vs. 6.12°). Finally, the precedence of head or trunk motion had no effect on the correlation between the perceived target position and the magnitude of either the head or the trunk rotations. The highest computed mean-between-subjects r^2 value was only 0.34, and it characterized the equation of the linear regression obtained when the perceived target position was plotted against the magnitude of the trunk rotations when the onset of the trunk motion occurred prior to that of the head rotation.

Discussion

Subjects were able to retrieve the position of the peripheral, extinguished visual target when the head (and gaze) remained stationary in space. They were also accurate in producing head movements towards this memorized visual target. Therefore, in the condition where the head was rotated to different positions with respect to the target (with or without simultaneous body rotations), it is unlikely that any errors in the perception of the target position were a consequence of a misperception of the target position or errors in producing head movements per se.

Subjects showed a remarkable precision in determining the position of the memorized visual target after orienting the head to different positions with respect to the target. The small spatial errors and variability suggest no or small errors in the different sensory and motor subprocesses involved in the task. The CNS is therefore capable of using the central and peripheral signals elicited during head motion to update the target position with respect to the head.

However, when the subjects were rotated during the voluntary head movements, the precision in the target position estimation markedly decreased. Indeed, the results showed a large variability in the perception of target position during simultaneous synchronous head and whole-body rotations. This large variability was observed when subjects were not informed about passive trunk-rotation occurrences as well as in the control experiment, in which body rotations occurred in every trial. The larger variability in the performance found in HTR than in HR suggests that the subjects actually perceived body rotations during the combined head-trunk rotations, rather than only perceiving head-on-trunk motions. The perception of a passive component in the head-in-space displacements is also evidenced by the results showing that the estimates of the target position in HR and in HTR were also different when they were referred with respect to the trunk. Indeed, without the perception of the trunk rotation in HTR, the subjects would have positioned the laser spot at the same position with respect to the trunk as in HR, that is close to 21°. Nevertheless, the perception of trunk rotations during the voluntary head movements did not allow the subjects to accurately determine the position of the target.

Several sources of information may have been combined to detect body rotations during head movements. This perception may originate from a mismatch between expected and actual vestibular signals or from a discrepancy between cervical and vestibular signals caused by the passive trunk rotations. Efference copy mechanisms from the voluntary neck muscle activation may have contributed to the perception of passive displacements of the head in space in providing some foreknowledge of the expected cervical and vestibular output given the voluntary head rotation the subject intended to perform. Cutaneous stimulation during body acceleration and deceleration and activation of internal somato-graviceptors, signaling body motion, could also underlie the perception of body rotations during the head movements [see Mittelstaedt (1995) and Mittelstaedt (1996) for a discussion of these somato-graviceptors].

In HTR, the onset of head movement preceded that of the trunk in about 60% of the trials. This presumably results from the lower inertia of the head compared to the inertia of the chair, which the experimenter had to overcome to rotate the subjects. However, the order of occurrence of the head and trunk motion had no significant effect either on the perceived target position or on the variability in the subjects' estimates of the extinguished target position following the combined head-trunk movements. This may suggest that the contribution of cervical and vestibular signals in updating space during the head rotation was not affected by whether or not the onset of the voluntary head movements occurred before or after the onset of the passive body rotation.

The subjects tended to overestimate the target position after combined head-chair movements when chair rotations occurred randomly or in every trial. This overestimation in the target position suggests that subjects underestimated the passive body rotations, hence changes in target-head relative positions. This type of error has also been found when subjects attempted to localize the position of a previously, peripherally flashed target after passive whole-body rotations without voluntary head rotations (Blouin et al. 1995a,b, 1997a).

Accurate encoding of a target location when the head-in-space position changes through head and body motion could only be obtained through vestibular-signal processing. Therefore, the results of the present experiment suggest that visual space cannot be updated accurately through vestibular signals during head rotations. The cervical signals generated during active head rotations presumably have no gating function on the vestibular signals, which could enable them to be better processed by the visuospatial systems in order to update target position during head-in-space motion.

The inaccuracy in processing vestibular signals to update visual space suggests that the almost ideal perception of the extinguished visual target position found when subjects produced voluntary head movements without simultaneous trunk motion could result from cervical signal processing. This would be in agreement with other studies showing important contributions of neck proprioception in visuospatial processes (Biguer et al. 1988; Blouin et al. 1995c, 1998, in press; Mergner et al. 1992; Nakamura and Bronstein 1993, 1995; Roll et al. 1991; Taylor and McCloskey 1991).

Results from the present experiments also support the recent hypothesis that determination of the magnitude of head-in-space motions and coding of a target position after such movements correspond to different cognitive tasks involving different neural substrates (Blouin et al. 1997a). Computing head-in-space motion can be considered to be a purely interoceptive task in the sense that the CNS, which is equipped with integrators (McFarland and Fuchs 1992; Robinson 1989), has the possibility of determining with relatively good accuracy the extent of head rotations in the dark without a fixed reference signal from the environment (visual or auditive, for instance). This possibility has been documented by several authors (e.g., Bloomberg et al. 1988; Blouin et al. 1995a,b,c, 1997a; Guedry et al. 1971; Israël 1992; Israël et al. 1993; Maurer et al. 1997; Mergner et al. 1991; Nakamura and Bronstein 1993, 1995). On the other hand, to encode a target position after head-in-space rotations, the vestibular signal has to be not only integrated over time, but it must reach, and be processed by, the systems involved in visuospace processing (e.g., the posterior parietal cortex) in order to keep trace of the target position with respect to the body during movement. Errors are likely to occur in this latter process. Therefore, according to this hypothesis, there are no inconsistencies between the experiments showing the possibility of determining the magnitude of passive whole-body rotations in the dark and those, like the present experiments, showing a large inaccuracy in updating visual space through vestibular signals during head-in-space movements.

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