Fusion of Visuo-ocular and Vestibular Signals in Arm Motor Control

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Guillaud, Etienne, Gabriel Gauthier, Jean-Louis Vercher, and Jean Blouin. Fusion of visuo-ocular and vestibular signals in arm motor control. J Neurophysiol 95: 1134–1146, 2006. First published October 12, 2005; doi:10.1152/jn.00453.2005. Keeping the finger pointing at an Earth-fixed object during body displacements can be achieved if compensatory arm movements counteract the effect of the rotation on the hand’s position in space. Here we investigated the fusion of signals that originated from systems having different neurophysiological properties (i.e., the visuo-oculomotor and vestibular systems) in the production of such compensatory arm movements. To this end, we analyzed the subjects’ performance in three conditions that differed according to the information they provided about relative target-body motion. This information originated either from the vestibular or visuo-oculomotor system, or from a combination of the two.

To highlight the integration of visuo-oculomotor and vestibular signals, we compared the arm response to motion frequencies presumed to allow or not to allow optimal vestibular and oculomotor responses. When they could be used in isolation, the ocular signals allowed long-latency but precise kinematics control of the arm movement, whereas vestibular signals allowed accurate motor response early in the rotation but their contribution declined as body rotation developed. Optimal performance was obtained throughout the whole movement and for all rotation frequencies when the visuo-oculomotor and vestibular signals could be used together. This increase in hand-tracking performance could not be explained by a unimodal model or an additive model of vestibular and ocular cues, even when using weighted signals. Rather, the results supported a functional model in which vestibular and visuo-oculomotor signals have different influences on the temporal and spatial aspects of hand movement compensating for body motion.

INTRODUCTION

Stabilizing the hand in space and reaching for an object in the environment during body motion are routine tasks. Some examples of such motor behavior are reaching for a button while walking and filling a glass at the tap while rotating the trunk. In the former case, the body motion assists the reaching movements; in the latter, the body motion can be considered as “noncooperative” and may imperil the goal of the arm action. The present study focuses on the control of arm movements during “noncooperative” body motions. To preserve the hand’s spatial goal in this situation, compensatory arm movements must be produced to counteract the effect of body motion on the hand’s position in space. For externally driven (i.e., passive) body displacements, when the direction, velocity, and amplitude of the body motion are unpredictable, counteradjustments of the arm cannot be controlled through feedforward processes. Rather, they might essentially rely on feedback processes, i.e., on the signals that provide information about body motion with respect to the hand’s spatial goal. In the present study, we consider the condition where subjects attempt to keep both their hand and gaze on a visual target during sudden passive whole body rotations in the dark. The signals most likely used to code body–target relative displacement during such behavior are those associated with eye movements (leading to gaze stabilization) and those resulting from body rotation. Our main concern here is to understand how these different signals contribute to the control of compensatory limb movements during body rotation.

Keeping the gaze directed at a visual target during whole body rotation in the dark is accomplished through the activation and cooperation of the vestibulo-ocular reflex system and the smooth pursuit system (Fukushima 2003; Schweigart et al. 2003; Vercher and Gauthier 1990). The retinal and oculomotor signals (i.e., proprioception and efference copy) thus generated during the eye movements can provide information about the target-to-body displacement to be used to control compensatory arm movements. When tracking a target with the eyes and the (unseen) hand, the hand usually lags the target (Gauthier et al. 1995; Honda 1990; van Donkelaar et al. 1997a,b). However, target motion frequency has a marked effect on tracking performance for both the eyes and the hand; indeed, performance degrades as frequency increases (Bock 1987; for a review see Xia and Barnes 1999).

The vestibular system provides information about the linear and angular displacements of the head and trunk (through neck muscle proprioception). The contribution of vestibular signals in the control of posture (Day et al. 1997; Nashner and Wolfson 1974), locomotion (Bent et al. 2000, 2004; Fitzpatrick et al. 1999), and eye movements (Angelaki 2004; Barnes and Eason 1988; Cohen et al. 1992; Lisberger and Sejnowski 1992; Zee 1981) has been extensively described in the literature. There is less documentation of the vestibular-related motor functions we are studying here, involving the control of arm movements during body motion. Still, some recent studies suggest that vestibular signals can provide information about the direction and velocity of the compensatory arm movements that need to be produced to reduce the effect of body motion on hand-in-space position (Bresciani et al. 2002a,b,c 2005; Feldman et al. 2003; Mars et al. 2003; Tunik et al. 2003). For instance, individuals who are passively rotated while reaching for a memorized target with no visual cue can modify their hand trajectory on-line to reach a target with small errors (Bresciani et al. 2002b, 2005). The recent finding showing that patients with vestibular deficits cannot maintain a steady-state...
hand movement while moving their trunks, in contrast with deafferented patients (Feldman et al. 2003; Tunik et al. 2003), also argues for a close link between vestibular signals and the arm motor system in such a task. 

Electromyographic responses to galvanic vestibular stimulation have been recorded in the triceps brachii muscles with latencies as short as 30–40 ms (Baldissera et al. 1990; Britton et al. 1993). On the basis of such latencies, it has been suggested that vestibular input reaches motoneurons by direct pathways (e.g., by the vestibulospinal and reticulospinal pathways; Britton et al. 1993; Fitzpatrick et al. 1999; Welgampola et al. 2001). Therefore during body motion, accurate and rapid compensatory arm movements can be triggered by vestibular signals. However, the capacity to process vestibular signals to control arm movements is likely condition specific. Indeed, the dynamic properties of the vestibular system’s components make the labyrinths unfit for detecting acceleration smaller than 0.05° s⁻² (Nashner 1971). Below this threshold, because of these high-pass transfer characteristics of the vestibular system, low rotation frequencies can be detected but are underestimated (Mergner et al. 1991).

Thus visuo-oculomotor and vestibular signals can contribute to the control of arm movements during body motion. According to weighted additive models of signals fusion (see for example Howard 1997; Mergner et al. 2001), the weights assigned to the vestibular and visuo-oculomotor cues could depend on the body rotational frequency. Visuo-oculomotor signals would be particularly efficient in controlling compensatory arm movements during low-frequency body rotations, whereas vestibular signals would be more efficient in high-frequency conditions (and thus with high acceleration). Therefore the compensatory arm movements during whole body rotations should be optimal in a large range of rotational frequencies as a result of visuo-oculomotor and vestibular signals integration. The goal of the present experiment was to test this prediction by analyzing arm motor response to different visuo-oculomotor and vestibular stimulations during relative target-to-body displacements. More specifically, to emphasize the integration of visuo-oculomotor and vestibular signals in arm motor control, we compared the arm response to stimuli having different frequencies. The low and high frequencies were selected on the premise that they allowed or did not allow optimal oculomotor or vestibular responses. Discussion on the nature of the visuo-oculomotor and vestibular signals fusion also required us to determine how the arm motor system responded, in our experimental context, to vestibular and visuo-oculomotor information when present in isolation.

METHODS

Subjects

Seven self-declared right-handed subjects (four men and three women) volunteered to take part in this experiment. Their average age was 26 yr (SD = 5). None of them had any history of vestibular or ocular disorders. They all had normal or corrected-to-normal vision. Before the experiment, the subjects gave their informed consent to participation in the study, which was performed in accordance with the ethical standards established in the 1964 Declaration of Helsinki.

Procedures

The experiment was carried out in darkness. Participants were seated on a chair positioned above the rotation axis of a motorized revolving platform (1.5 m diameter). The chair could be affixed either directly to the platform (Fig. 1A) or to a horizontal set of Earth-fixed rails placed 15 cm above the platform (Fig. 1B). In the latter case, the chair (and the subject) remained motionless during platform rotation, the rotation being used here only to move the target around the subjects, as we will detail below. The platform was rotated by a servomotor whose speed was controlled by a Smart Motor Control Card (Baldor SMCC). The platform’s angular position was returned to the computer by the axis control card. A headrest attached to the seat prevented head-on-trunk displacement. Participants wore audio earphones that diffused white noise to mask out auditory spatial reference cues.

The position of the subject’s right index finger was detected by a 6-degree-of-freedom electromagnetic sensor (Polhemus Fastrak) taped to the tip of the index finger (the emitter was positioned 10 cm above subject’s head). Because magnetic fields are sensitive to metallic environments, all the elements positioned inside the magnetic field were made of wood or plastic. This precaution ensured good linearity of the recording system over the working space of each experimental condition (as tested before the experiment both with and without chair rotation). With this system, the absolute position of the finger could be measured with accuracy within 1 mm. Horizontal eye movements were measured using an electro-oculographic device (Lablinc V bio-amplifier manufactured by Coulbourn). All signals were recorded at 120 Hz using a Keithley (AD-win pro) A/D converter device.

All visual information (e.g., target, fixation light) was provided to the subjects with light-emitting diodes (LEDs, 3 mm in diameter) located 15 cm above a semireflecting glass board (1.2 × 1 m) resting horizontally at neck level. A narrow board positioned vertically between the observer and the LEDs prevented direct vision of the LEDs, which appeared as virtual images 15 cm beneath the glass, i.e., slightly below the participant’s shoulders; thus tactile contact with the targets (or fixation point) was not possible. Vision of the hand was prevented by a black sheet placed under the glass (this procedure does not change the reflective properties of the glass). Distance between the subject and the target was adjusted to obtain a comfortable arm position when the finger was positioned on the target (it was usually around 55 cm).

Of the three conditions that were run, two involved rotating the subjects in front of an Earth-fixed target and one involved rotating the target in front of the immobile subjects. Rotation amplitude was always 60°. The subject’s task was to maintain the right index finger on the target during the relative target–body motion. The initial target position was always 30° to the left of the participants’ midsagittal

A Vestibular and combined conditions

B Ocular condition

FIG. 1. Schematic representation of the setup used in the ocular, vestibular, and combined conditions. In both ocular and vestibular conditions, the subject was rotated and the target was Earth-fixed. In the ocular condition, the subject, seated on the chair fixed on the tracks above the rotating platform, remained stable and the target was rotated by the platform.
plane and the final position always 30° to the right. It follows that the relative rotation direction between the body and the target was the same in all conditions, therefore requiring identical arm motor responses in the subject's body reference frame. Hereafter, "tracking arm movements" will refer to the movements produced by the subjects to keep the hand either stationary in space during body motion or on the moving target when the body was still.

Each trial was preceded by a preparatory period during which the target and an LED located at the tip of the index finger were simultaneously visible. During this period, the subject extended the arm to position the index finger at the starting position. The finger LED was lighted for 3 s. The time between the offset of the finger LED and the onset of the rotation was randomized, at 300, 750, or 1750 ms, between trials to avoid movement onset prediction. Approximately 2 s after the rotations, the platform returned, still in darkness, to its initial position using the same velocity profile as that used for the initial rotation. During the return phase, subjects positioned their pointing hand on their thigh.

**Vestibular condition**

In the vestibular condition, the chair was attached to the revolving platform (Fig. 1A). Its motion rotated subjects around their vertical axes, principally stimulating the horizontal semicircular canals of the labyrinths. The subjects were instructed to keep their index finger on the extinguished Earth-fixed target during the rotation (Fig. 2, middle). To minimize eye movements likely to result from vestibulo-ocular reflex activation, subjects gazed at a platform-fixed LED during rotation (a condition allowing subjects to determine body rotation with good accuracy; Bloomberg et al. 1988; Blouin et al. 1995c; Israël et al. 1993). This LED was positioned 35° to the left of the subjects (i.e., 5° to the left of the target before rotation). Therefore in this condition, the required compensatory arm movements were assumed to be mainly determined through vestibular information.

**Ocular condition**

In the ocular condition, the chair was fixed on the set of rails above the rotating platform and therefore remained motionless (Fig. 1B). The target’s LED was attached to the upper end of a vertical rod bolted to the platform. Its virtual image remained visible during the rotations. The subjects’ task consisted in pursuing the rotating target with their arm and eyes (Fig. 2, right). In this condition, information about the arm movements required to keep the finger on the target was derived from visuo-oculomotor signals generated during the pursuit eye movements.

**Combined condition**

The setup in the combined condition was identical to that used in the vestibular condition (i.e., the chair was fixed to the platform). However, here, the Earth-fixed target remained visible during the rotation. Subjects were instructed to keep their index finger and eyes on the target during body rotation. Therefore the required eye movements were similar in amplitude and dynamics to those induced in the ocular condition. However, they were not controlled through similar neural processes because of the contribution of vestibular signals in this combined condition (Robinson 1981). We shall use the term “pursuit eye movements” when referring to the ocular movements in both the ocular and combined conditions. On the other hand, the vestibular information in the combined condition was identical to that generated in the vestibular condition. As a consequence, in the combined condition, both the visuo-oculomotor and vestibular signals could convey the information necessary for controlling compensatory arm movement during body rotations.

**Rotation velocity profiles**

In all conditions, the servomotor generated 60° platform rotations with a bell-shaped velocity profile very close to a cosine (Fig. 3). We varied the rotation’s acceleration and velocity because these are known to affect both the vestibular system’s efficiency in detecting body motion and the quality of the pursuit eye movements. Rotations will be referred to according to their frequency (in accordance with the studies on the vestibular functions and on the smooth pursuit eye movements). Each rotation described a half-cycle of 60° in amplitude in the half-time of whole cycle. The rotation frequencies tested were 0.05, 0.07, 0.08, 0.1, 0.12, 0.15, 0.2, 0.23, 0.26, 0.3, 0.32, and 0.34 Hz. Their distribution was nonlinear so as to obtain more data for frequencies expected to have a greater effect on subjects' performance (i.e., the lowest and highest frequencies). Rotation durations were a function of the rotation frequencies. They ranged between 1.47 and 10 s (duration of the highest and the lowest frequencies, respectively).

Each condition was composed of 96 trials, i.e., eight trials per rotation frequency. The order of presentation of the conditions was randomized between subjects. The order of presentation of the frequencies was randomized within each condition. Each subject was tested in only one experimental condition per day.

**Data processing**

The raw signals from eye, finger, and platform position signals were low-pass filtered (zero-phase forward and reverse digital But-
Angular index finger position was computed on the basis of the Cartesian coordinates provided by the electromagnetic sensor and adjusted to have a value of zero when the finger was at the starting position (just before the onset of rotation). Because the required arm movements were similar with respect to the trunk under all conditions (see Fig. 2), angular index finger position variations were computed with respect to the trunk.

Delays in the visuo-oculomotor system may cause accumulation of retinal errors when tracking a visual target, especially when the target moves at high velocity. The strategy developed by the oculomotor system to keep the target’s image on the high-acuity foveal region when retinal velocity errors reach a certain level is to combine smooth eye movements with rapid catch-up saccades (de Brouwer et al. 2002; Lisberger et al. 1987). In the present study, analyses of the tracking eye movements were performed on the portions of the eye velocity traces without saccades. When saccades occurred, they were removed from the traces and substituted by a “smooth pursuit” component using an interpolation procedure. First, saccades were identified when the eye movement velocity differed from the target velocity by 50° s⁻¹. Then backward and forward searches were performed to detect the onset and offset of the saccades, respectively. The beginning of a saccade was defined as the point 8 ms before the eye velocity crossed the required velocity plus a limit of 2 SDs (the SD was computed before stimulus displacement when the eyes were motionless; mean SD across subjects = 5° s⁻¹). The end of a saccade was defined in a similar manner. The portions of the eye velocity showing a saccade were removed. Eye velocity was averaged both before and after the saccade on 24-ms time ranges. Difference between the computed velocities was used with the saccade duration to compute a constant average acceleration. The removed portion was then replaced by a straight line generated on the basis of this acceleration. This method was inspired by methods used in previous studies (Barnes 1982; Engel et al. 2000; Kanai et al. 2003).

**Measured variables**

**VELOCITY RATIO.** Dynamic precision of a pursuit movement can be evaluated for any given moment during the course of the movement with the instantaneous velocity ratio. The velocity ratio of ocular and manual pursuits was computed using the equations ωhand(t)/ωstimulus(t) and ωvest(t)/ωstimulus(t), which were, respectively, the angular velocity quotients of the hand and the eyes, over the stimulus velocity (body or target rotations). However, velocity ratio does not progress with a linear function. For instance, the VR value would be 0.5 if the stimulus moves twice as fast as the hand but it would be 2 if the hand is moving twice as fast as the stimulus. This nonlinearity was substantially reduced transforming VR into its log base 2. With this transformation, similar stimulus and hand velocities would be associated with a Log (VR) of 0, Log (VR) of −1 would indicate that the stimulus moves twice as fast as the hand, and Log (VR) of 1 would indicate that the hand is moving twice as fast as the stimulus. Log (VR) was used in the statistical analyses to solve the problem of the VR’s nonlinearity, and the VR values were plotted on a semilogarithmic plot in the figures (Figs. 4, 7, and 10).

**VELOCITY GAIN.** The velocity of the tracking movement can match the velocity of the moving stimulus without being perfectly in phase with it. Because of the latency or the delay of the studied sensorimotor system, movements can lag behind the stimulus. In such a case, the VR value can reveal errors even though subjects are tracking with the right speed that is moving at a nonconstant velocity, as in the present experiment. For these reasons, velocity gains were also calculated after phase-shift compensation. They correspond to the velocity ratio computed on signals after phase-shift compensation.

The phase lag was computed, for each trial, by cross-correlation in the time domain on the entire signals of angular velocities of the stimuli and the effectors, i.e., either the hand or the eyes. An optimization routine (based on the Matlab “xcorr” function) computed for each trial the correlation between both signals for each possible phase shift (with 8-ms steps) in both directions. The phase lag was the induced phase shift for the best-measured correlation. Then, the effect of the lag on the effector displacements was compensated for extracting the lag value from the data. A positive lag value indicates that the movement lags behind the stimulus; a gain close to 1 after phase-shift compensation would indicate that the subject tracked the target at the right speed. Conversely, a gain different from 1 would indicate that the dissimilarity between the compared signals is not only of temporal origin but also arises from the fact that the effector is not tracking the stimulus with the appropriate velocity. In the present experiment, a greater lag was expected between the finger and the target in the ocular condition than in the vestibular condition. The phase lag compensation should therefore affect to a greater extent the results obtained in the ocular condition than in the vestibular condition.

**ANGULAR ERROR AND REACTION TIME.** In all conditions, finger and target position signals with respect to the trunk were used to analyze movement accuracy. The current angular error was defined as the angle separating the hand or the eyes (the latter in the ocular and
Movement onsets were detected using a 1° s⁻¹ criterion (backward search from peak velocities). Movement decomposition

For each trial, analyses were performed on stimuli movement segments of varying lengths. The smallest segment was one tenth of the entire movement; the largest was the whole movement. These analyses revealed that the VR varied during the movements. The mean VR of three of the analyzed segments appeared to be most representative of subjects’ performance under different experimental conditions and will be presented here. These segments are: total movement and the acceleration and deceleration phases of the stimuli. Because any small disparities between target and finger motion (in relative velocity) at the beginning and the end of the movements had an appreciable effect on the resulting VR values, the first tenth and the last tenth of the movements, respectively, were excluded from acceleration and deceleration phase analyses.

Statistical analyses

Repeated-measures ANOVAs were used to test the effects of the three experimental conditions and of the 12 rotation frequencies on the dependent variables. The only difference between the velocity gain and VR variables was the phase-shift suppression during the gain computation. Using the phase-shift cancellation as a new variable with gain and VR variables was the phase-shift suppression during the gain computation. Nevertheless, in these conditions, the VR was significantly smaller (although marginally) at 0.05 Hz than at frequencies >0.08 Hz (P < 0.05). Conversely, in the ocular condition, the rotation frequency had a substantial effect on the VR during the acceleration phase. The VR, which was 0.92 for the lowest frequencies (0.05 and 0.07 Hz), started to significantly decrease as rotation frequencies increased at 0.15 Hz (P < 0.03), decreasing to 0.21 for the highest frequency. The ANOVA showed that this frequency × condition interaction was significant (F(22,132) = 59, P < 0.001, LSD = 0.09 [from the log (VR)]). VR was significantly lower in the ocular condition

Hand movement velocity ratio

The rotation frequencies and the conditions had dramatic effects on tracking arm movements when VR was averaged on the whole stimulus movement (Figs. 4 and 5). This was confirmed by the significant condition × frequency interaction \{F(22,132) = 4.17, P < 0.001, LSD = 0.19 [from the Log (VR), Fig. 4A]\}. Post hoc analyses showed that VR increased in both the ocular and the vestibular conditions as rotation frequencies increased (values of P < 0.05). This increase started at a moderate frequency in the ocular condition (0.23 Hz) and from the smallest tested frequency in the vestibular condition (0.05 Hz). Conversely, in the combined condition, the VR remained stable at around 0.8, with VR significantly greater at 0.2 Hz than that at 0.07, 0.08, and 0.1 Hz (P < 0.03). A main effect of the experimental conditions was also observed. VR was significantly greater in the ocular than in both the combined condition (for all frequencies but 0.2 Hz, P < 0.05) and the vestibular condition (for all frequencies, P < 0.05). Finally, in eight of the 12 tested frequencies, VR was statistically different in the vestibular and combined conditions (P < 0.05; no differences were found at 0.07, 0.1, 0.3, and 0.32 Hz).

The effects of frequency and condition on the VR differed principally between the acceleration and deceleration phases of the hand-tracking movements (Fig. 4, B and C). During the acceleration phase, hand tracking was of good quality under both the vestibular and combined conditions in all tested rotation frequencies, where VR was close to 1 (Fig. 4B). Nevertheless, in these conditions, the VR was significantly smaller (although marginally) at 0.05 Hz than at frequencies >0.08 Hz (P < 0.05). Conversely, in the ocular condition, the rotation frequency had a substantial effect on the VR during the acceleration phase. The VR, which was 0.92 for the lowest frequencies (0.05 and 0.07 Hz), started to significantly decrease as rotation frequencies increased at 0.15 Hz (P < 0.03), decreasing to 0.21 for the highest frequency. The ANOVA showed that this frequency × condition interaction was significant (F(22,132) = 59, P < 0.001, LSD = 0.09 [from the log (VR)]). VR was significantly lower in the ocular condition
than in the vestibular and combined conditions for frequencies >0.1 Hz (P < 0.03).

The ANOVA also showed a significant frequency × condition interaction on the tracking mean VR during the deceleration phase (F(22,110) = 9.47, P < 0.001, LSD = 0.25 [from the log (VR)]). The effects were radically different from those observed in the acceleration phase (see Fig. 4C). In the vestibular condition, hand-tracking movements were characterized by small VR values in the deceleration phase, as small as 0.40 in the lowest rotation frequency. The VR slowly increased as the frequency increased, but remained of small magnitude until the frequencies reached high values (0.32 Hz). Above 0.26 Hz the VR increased considerably, reaching 1.2 at 0.34 Hz (significant increase from 0.08 Hz, P < 0.002). In the ocular condition, VR was higher than that in both of the other conditions for all frequencies during the deceleration. VR increased as rotation frequencies increased, contrary to the acceleration where it decreased. It was around the appropriate value of 1 in the lowest frequencies (i.e., 0.05, 0.07, and 0.08 Hz) but reached a value as high as 2.2 in the highest tested value of 1 in the lowest frequencies. Post hoc analyses showed that the lags were significantly higher in the ocular condition than in both the vestibular and the combined conditions for all frequencies (P < 0.05) but the two lowest frequencies in the latter condition. In the ocular condition, the lags remained stable around 130 ms whatever the frequency, where post hoc analyses showed a significant difference only between the lags measured in the 0.07 Hz (55 ms) and 0.34 Hz (195 ms) conditions (P < 0.02).

Gain and VR comparison resulted in a triple interaction shift cancellation × condition × frequencies in the acceleration phase [F(22,110) = 43.12, P < 0.001, LSD = 0.1 (from the log of VR and gain)] and in the deceleration phase [F(22,110) = 26.6, P < 0.001, LSD = 0.07 (from the log of VR and gain)]. Occurrence of phase shift had no or only small effects on the VR in the vestibular and combined conditions but had a marked effect in the ocular condition. Indeed, in the ocular condition, phase-shift compensation dramatically reduced and cancelled out the frequency effect observed in the acceleration and the deceleration phases, respectively (Fig. 7, left). Post hoc analysis showed that VR and gain significantly differed in all frequencies of the ocular condition but the smallest (i.e., 0.05 Hz, P < 0.01). After phase-shift compensation, the tracking velocity gain was slightly smaller than 1 in the acceleration phase (especially at high frequencies) and very close to 1 in the deceleration. Therefore the poor tracking quality observed in the ocular condition was mainly attributed to a lag between the stimulus motion and the hand response.

In the acceleration phase of the vestibular condition, VR and gain differed significantly in the lowest frequencies only (from 0.05 to 0.15 Hz, P < 0.015), where VR was closer to 1 than the gain (Fig. 7, middle). This suggests that the errors observed in low-frequency conditions resulted from an inappropriate hand-tracking velocity rather than from a simple delay between the hand and the stimulus. Greater VR with respect to the gain is in agreement with the results of the negative lags showed

Hand lags and hand movement gain after phase-shift compensation

Compensating for the phase shift between hand and target motion velocity signals allowed us to determine the degree to which the velocity ratio errors revealed in the previous analyses were attributed to lags between arm and stimulus displacements, or rather to inappropriate velocity of the hand movement. Here, lags refer to the phase shifts during task executions, which can differ from latencies (or reaction times), which constitute the initial delays between the initiation of target and hand movements.

The frequency and the condition had appreciable effects on the lags (see Fig. 6). This effect was attested to by the significant frequency × condition interaction [F(22,132) = 8.52, P < 0.001, LSD = 77 ms]. For the combined condition alone, the lags remained stable around the null value in all tested frequencies (no significant difference between frequencies, P > 0.05). For the vestibular condition, the measured lags showed that the hand led the stimulus in the lowest tested frequencies. The lag values were significantly lower in the vestibular conditions than in the combined condition below 0.12 Hz (P < 0.05). For this frequency and also frequencies that were higher, the lags were not statistically different between these conditions and were close to 0. In the vestibular condition, movement execution was of good quality during the initial part of the movement (as attested by VR analyses). However, the capacity to determine body rotation diminished during the deceleration. The hand started to decelerate slightly before the stimulus and came to a rest while the stimulus was still moving (see Fig. 5 for an illustration). Therefore the hand...
above for the low frequencies in the vestibular condition. Because subjects underestimated body rotation velocity for these frequencies, they started to decelerate and came to a rest before the stimulus. In the vestibular condition, phase-shift compensation had no significant effect on VR during the deceleration phase for frequencies between 0.12 and 0.3 Hz ($P > 0.05$), but significantly affected VR for the other frequencies ($P < 0.05$) (because the differences were smaller than 0.055, they can hardly be seen in Fig. 7 because of the scales of the graphs). Therefore the gain remained small in all rotation frequencies but the greatest (>0.26 Hz).

Finally in the combined condition, the gain and VR remained relatively stable between 0.8 and 1 in both the acceleration and the deceleration phases (Fig. 7, right). The phase-shift compensation had only moderated effects on the VR. Post hoc analyses showed that the VR was significantly smaller than the gain at 0.2 Hz ($P < 0.03$) in the acceleration phase, and was significantly greater than the gain between 0.15 and 0.25 Hz in the deceleration phase. However, the differences between VR and the gain did not exceed 0.08. As can be seen in Fig. 7, the gain in the ocular condition was frequently closer to 1 than both the gain and VR in the combined conditions. This was the case for all frequencies in the deceleration phase and for all frequencies smaller than 0.12 Hz in the acceleration phase, with a significant difference between both conditions at these frequencies ($P < 0.05$).

**Hand-tracking angular error**

The error in hand movement tracking varied as a function of the stimulus frequency and the experimental condition. This can be seen in Fig. 8, which, for the purpose of clarity, presents the errors obtained with only the three lowest and the three largest rotation frequencies. In the ocular condition, a small error was observed throughout the movements performed with low rotation frequencies. For the large rotation frequencies, the errors rapidly increased during the initial phase of the movement (i.e., acceleration) and reached great magnitudes (up to $-20^\circ$). However, these errors decreased rapidly during the deceleration phase and had positive values toward the end of the movements (hand over tracking the target). For the ocular condition, the variations of the errors in the acceleration and deceleration phases are thus in concordance with a lag in the arm motor response with respect to the moving target.

In the vestibular condition, the stimulus frequencies had only a negligible effect on the hand angular error during the acceleration phase (mean over tracking of $1.5^\circ$). However, a marked frequency effect was observed during the deceleration phase (see Fig. 8, middle). For the greatest frequencies, the hand exceeded stimulus position, as attested by the positive errors that developed in the second half of the movements. At lower frequencies, on the contrary, the hand largely lagged behind the target (errors reaching $17^\circ$ in the lowest frequency).

In the combined condition, similarly to the vestibular condition, the angular error was small during the initial phase of the movements. Errors developed during the deceleration phase, in which the hand was lagged by the target. This error increased as rotation frequency decreased.

An ANOVA performed on the terminal hand error revealed a significant frequency $\times$ interaction [$F(22,132) = 7.73, P < 0.001$, LSD = 3.4°]. The magnitude of the movements increased as the frequencies increased in all conditions, although this increase was greatest in the vestibular condition (see Fig. 9A). Post hoc analyses showed that the errors significantly increased from 0.07 Hz in the vestibular condition, and from only 0.15 Hz in both the ocular and combined conditions.
The difference between the terminal angular errors for low and high frequencies was as high as 23° in the vestibular condition (from −17 to 6°, respectively). This difference was only 7° in the ocular condition, being −4 and 3°, respectively, for the lowest and the highest frequencies. In the combined condition, the difference between the terminal angular errors for low and high frequencies was also 7° (from −11 to −4°). The effect of rotation frequency on the terminal hand error was thus smaller in both conditions where subjects tracked the target with the eyes than that in the vestibular condition, where no pursuit eye movement was required. These errors, dependent on the rotation frequencies, were smallest in the ocular condition.

**Reaction time**

For the lowest rotation frequencies, the required finger velocity at movement onset was too small to be distinguished from the velocity signal issued from hand oscillation while subjects attempted to keep the hand still in space. We surmise that this caused late detection of finger movement onset and therefore an overestimation of arm reaction time for the movements performed at low rotation frequencies. Consequently, the absolute reaction time values obtained in the lowest rotation frequencies are presumably not very representative. This bias decreased when the frequencies increased. However, because this bias is similar across all experimental conditions, it should have no effect on the difference in reaction times between the different conditions. The mean arm movement reaction time was higher in the ocular condition (mean = 434 ms) than that in both the vestibular and combined conditions [global mean = 95 ms; F(2,12) = 98.3, P < 0.001; LSD = 60 ms]. No significant difference appeared between reaction times in the vestibular and combined conditions (P > 0.05; see Fig. 9B).

**Ocular velocity ratio**

In both the ocular and the combined conditions, subjects tracked with their eyes the lighted target that moved with respect to their body. For these conditions, ocular movements were analyzed to determine whether the quality of pursuit eye movements influenced the quality of hand-tracking movements. Eye movement velocity ratio could not be computed in the vestibular condition because the subjects were to gaze at a
The lowest frequencies, the ocular VR was close to 1 in both the acceleration and deceleration phases of the vestibular and combined conditions. However, VR was affected by the increase in frequencies (Fig. 10). The effect was similar to that observed on hand-tracking movements: during the acceleration phase, the ocular VR decreased with the frequency, whereas in the deceleration phase, it increased. The variations as a function of frequency of the ocular VR were greater in the ocular condition than in the combined condition. This was revealed by the significant frequency x condition interactions in both the acceleration phase \(F(11,66) = 11.5, P < 0.001, \text{LSD} = 0.14 \text{[from the log (VR)]}\) and the deceleration phase \(F(11,44) = 2.3, P < 0.05, \text{LSD} = 0.12 \text{[from the log (VR)]}\).

During the acceleration, the ocular VR was generally closer to 1 in the combined condition than that in the ocular condition. This was confirmed by the post hoc analyses that showed that VR was significantly greater in the ocular condition than that in the combined condition in all frequencies greater than 0.07 Hz but 0.12 Hz. During the deceleration phase, VR values of both conditions differed significantly at 0.23, 0.32, and 0.34 Hz; VR was closer to 1 in the combined condition than in the ocular condition. Therefore the quality of pursuit eye movement was generally greater when vestibular stimulation was present than when it was absent. Increasing rotation frequency diminished the quality of pursuit eye movement in both conditions, but the presence of the vestibular signal in the combined condition reduced this effect.

**FIG. 10.** Velocity ratios (VRs) of eye tracking in all tested frequencies during the acceleration (A) and deceleration (B) phases, in both conditions where eye movements were required. Plotted values are the logs of the VR; the actual VR values correspond to the left axis, which is labeled with a logarithmic scale; and the logs of the VR values correspond to the right axis, which is labeled with a linear scale. Stimulus frequency significantly affected the eye tracking VR in both the ocular and combined conditions and in both phases of the tracking responses. Vertical bars indicate between-subject SDs.

The main goal of this experiment was to determine the contribution of vestibular and visuo-oculomotor signals in controlling compensatory arm movements produced to prevent hand-in-space motion during whole body rotations. To achieve this, we compared the quality of arm movements in conditions where either or both signals were available. The results showed that vestibular and visuo-oculomotor information had different effects on the temporal and spatial characteristics of the hand tracking. These differences accentuate the interest of studying their complementarities in controlling arm movements. We will summarize and comment on the respective specificities of ocular and vestibular control of arm movements in the present experimental context. By comparing subjects’ performance when vestibular and visuo-oculomotor signals were available to when they could only be used in isolation, it will then be possible to discuss the nature of the vestibular and visuo-oculomotor fusion in arm motor control.

**Vestibulo-manual control**

Over the entire movement execution, subjects’ hand-tracking movement underestimated stimulus rotation by about 20% in the vestibular condition. Similar underestimation has been reported in vestibularly evoked perception of self-motion magnitude when no feedback on accuracy was given to the subjects (Blouin et al. 1995a,b,c, 1997; Féry et al. 2004; Israël et al. 1993; Nasios et al. 1999). However, analyses of the entire movements masked a clear and marked difference between the quality of tracking during the acceleration and the deceleration phases of the movements. During the acceleration phase, the arm movement matched the spatiotemporal characteristics of the body motion, whatever the rotation frequency. The null (or negative) lags and low reaction times observed in this condition confirm the short latency of vestibularly evoked arm motor responses reported in previous studies (Baldissera et al. 1990; Bresciani et al. 2002b; Britton et al. 1993). During the deceleration phase, however, the tracking movement VR was generally low, ranging from 0.4 to 0.6 for rotation frequencies smaller than 0.23 Hz. Cancelling the phase shift between arm and target signals had no positive effect on the velocity gain. Therefore the low VR observed during the deceleration phase was attributed to inaccuracy in detecting stimulus motion rather than to a lag between stimulus and hand motion. Body rotation underestimations during low rotation frequencies have already been reported and explained by the high-pass transfer characteristics of the vestibular system (Fernandez and Goldberg 1971; Mergner et al. 1991). Interestingly, this effect was observed only in body deceleration in the present experiment. Errors in processing vestibular signals during body deceleration could thus explain the underestimation of vestibularly sensed passive whole body rotations previously reported, even during moderately high rotation frequencies.

The fact that the body rotation frequency significantly affected the tracking arm movements during the deceleration phase only, and not also during the acceleration, was somewhat unexpected. The small tracking errors observed during the acceleration combined with the large rotation underestimation at low and moderate frequencies during the deceleration could suggest that perception of body displacement is more accurate for transient vestibular stimulations than for sustained stimu-
lations. Also, because attentional resources are required to accurately monitor changes in body orientation through vestibular inputs (Yardley et al. 1999), it is also possible that the subjects’ attentional level was greater at the beginning of the trials—to detect the onset and the dynamic properties of the body rotations—than afterward. The fact that mental state can have an influence on the VOR gain (McKinley and Peterson 1985) gives support to this possibility. Intervention of cognitive processes for detecting low-frequency body rotations was previously suggested by Becker and colleagues (2000).

Passive forces could also have contributed to the better tracking accuracy during the acceleration phase than during the deceleration. According to such a scenario, subjects could have similarly underestimated body rotation during the acceleration and deceleration phases (except in the highest rotation frequencies). However, the underestimation during acceleration could have been compensated for by the strong effect of muscular stretching while the shoulder was returning toward its neutral position. Indeed, during the acceleration phase, the subjects had to move the arm from a 30° contralateral position to a straight-ahead position. Therefore muscular stretches acted in favor of returning the arm toward the central direction, that is, in a direction similar to the motor task requirements. Here, the vestibular signals would ensure accurate detection of rotation onset but not an accurate spatial detection. Because of the arm’s inertia, the rotation of the body is likely to have caused stretching of the upper limb muscles. This could also have provided the CNS with short-latency proprioceptive information about body motion. Moreover, sensory inputs from graviceptors embedded in the abdominal viscera are known to give information about body rotation (Mittelstaedt 1992, 1995). Therefore it is likely that nonvestibular information contributed to the early arm-tracking response during the whole body rotations.

However, the tracking arm movement cannot be explained only by the arm’s viscoelastic properties or other passive forces such as the arm’s inertia that, by nature, act in such a way as to stabilize the hand in space during body motion. The fact that the reaction times of the arm movement with respect to the trunk were not null in the vestibular condition suggests delays in sensorimotor control, which are a signature of an active control of the arm movement by the CNS. Despite the fact that the forces applied to the arm during the deceleration phase were similar in both the vestibular and the combined conditions, a frequency effect was found only in the vestibular condition. This suggests that the control of the tracking movements involved active sensorimotor processes by the CNS. The slight overtracking found in the lowest frequencies of the vestibular condition also argues for an active control of the movement. Active arm movement control based on vestibular information has been evidenced in numerous studies (Bresciani et al. 2002a,c, 2005; Feldman et al. 2003; Mars et al. 2003; Tunik et al. 2003). Among these studies are those that have shown on-line modifications of the arm reaching trajectory after galvanic vestibular stimulation in conditions where the body was kept steady (Bresciani et al. 2002a,c). Adaptive modifications of the transfer function between vestibular input and the arm motor output have recently been shown to have a substantial effect on the accuracy with which subjects can both keep the arm stationary in space during body rotations and reach for memorized visual targets during such rotations (Bresciani et al. 2005). The fact that the vestibulo-manual relationship is under adaptive control provides further evidence of a tight link between vestibular and arm motor systems and suggests active control by the CNS of the arm movement during body motion.

**Oculo-manual control**

The way that oculo-manual tracking was affected by the stimulus frequencies is in accordance with the published literature. The accuracy with which subjects controlled their arm movements on the basis of visuo-oculomotor signals varied in relation to rotation frequency and the phase of the movement. The acceleration phase of arm movements in response to high-frequency rotations was characterized by a small velocity ratio. On the contrary, during the deceleration phase, the velocity ratio was too high and the hand preceded the decelerating target in space. The fact that the velocity gain was close to 1 in both movement phases after phase-shift compensation confirmed the lag’s major role in the arm tracking error. Therefore hand and target movements had close kinematic characteristics, but were separated by a great temporal delay (the target leading the hand by 130 ms, on average). This is in accordance with the observation that the hand rapidly lagged behind the stimulus (errors ≤20°) during the acceleration phase of the movement but was close to the target at the end of the movement (final angular errors were <4°). Thus the arm motor system was able to use the visuo-oculomotor signals generated during the pursuit eye movement to produce arm movements that matched target velocity. However, the overall tracking performance dramatically declined in high-frequency conditions because of the known long latency of the oculo-manual system. For instance, hand RT, which was 335 ms slower in the ocular condition than in both conditions with body rotations, was particularly harmful to the subjects’ performance when they were confronted with short stimulus displacements (1.5 s for the shortest). The arm inertia, acting against the movements in the ocular condition, likely contributed to the large hand-tracking RTs that were observed in this condition. The fact that the lags were smaller than the RTs suggests that the effect of inertia was compensated for during the course of the movement. Nevertheless, large lags were observed in all tested frequencies of this condition, even in those that resulted in long movement durations (≤10 s). Theoretically, in these trials, subjects had enough time to compensate for the hand-tracking RTs during the course of the movement. Therefore the lags computed in the ocular condition likely resulted from latencies in the visuo-oculomotor arm system rather than from long RTs.

**Vestibular and ocular complementarities in arm movement control**

Overall, the hand-tracking performance was of good quality when the visuo-oculomotor and vestibular signals could provide information about the change of the relative target-body displacement. This was true for both the acceleration and deceleration phases of the movements and in all tested rotation frequencies contrary to what was observed in both the ocular and vestibular conditions. It clearly appeared that errors in kinematics were minimized when the visuo-oculomotor and
vestibular sources of information were jointly available (Fig. 5). In the combined condition, the arm-tracking movement was more closely related to the spatial characteristics of the stimulus than in the vestibular condition (especially during the deceleration), and the hand movement temporal parameters matched to a greater extent those of the stimulus than in the ocular condition.

The question then arises as to whether the increased hand-tracking performance in the combined condition can be explained by a unimodal model or an additive model of vestibular and visuo-oculomotor cues. Results showed that lags and reaction times of the arm-tracking response in the combined condition (around 0 and 100 ms, respectively) were similar to those observed in the vestibular condition (Figs. 6 and 9). They were far from corresponding to the averaged values measured when ocular or vestibular cues were available only in isolation. On the other hand, the kinematics profiles of the tracking movements (revealed by the gain, i.e., after phase-shift compensation) in the combined condition resembled those of the ocular condition; they did not correspond to the average performance observed in the ocular and vestibular conditions. These results appear to contradict both unimodal and additive models of vestibular and visuo-oculomotor signals. However, one may wonder whether the additive model fails simply because a response lag was needed to overcome the limb’s inertia to initiate the tracking arm movement in the ocular condition but not in the combined and vestibular conditions. However, such a hypothesis is not supported by the fact that the duration of the target motion was sufficiently long to fully compensate for the tracking reaction time in most of the stimulus frequencies (e.g., stimulus durations ranged between 2 and 10 s in eight out of 12 frequencies), and by the fact that averaging performance in the ocular and vestibular conditions after removing the lag between the hand and the stimulus still generates different kinematics profiles with respect to those observed in the combined conditions. Also arguing against an additive model of ocular and vestibular signals integration is the fact that, for frequencies greater than 0.34 Hz, the VR values and the gains of the combined condition were even smaller than those in either the ocular or vestibular condition. These observations argue against an additive model, even when using weighted signals.

In the combined condition, because no phase lag was present, thanks to the vestibular contribution (presumably in combination with nonvestibular agents such as passive forces), both spatial and temporal errors were reduced. Our results therefore suggest that temporal and spatial parameters of the hand-tracking movements during whole body rotation are specified independently using different signals. Temporal parameters would be mainly adjusted on the basis of vestibular signals, and spatial parameters would be essentially adjusted on the basis of visuo-oculomotor signals. However, the fact that the VR was not optimal in the combined condition, contrary to the gain in the ocular condition (i.e., after phase-shift compensation), suggests that the multisensorial integration of the visuo-oculomotor and vestibular signals is not perfect, but rather is subject to errors (as opposed to the optimal numerical computation used to compensate for the phase shift in the ocular condition’s gain computation).

In the combined condition, predictive mechanisms are likely to have contributed, along with the vestibular and visuo-oculomotor signal processing, to the zero lag stimulus tracking by the hand. The control of manual and ocular tracking movements based on prediction of the target motion has long been recognized (Bahill and McDonald 1983; Poulton 1981; Vercher and Gauthier 1992; Xia and Barnes 1999). The prediction is known to be enhanced when target motion is highly predictable, as the sinusoidal velocity profile used in this experiment was. However, the effect of prediction should be greater during the deceleration than during the acceleration because the dynamic characteristics of the former can be inferred by those of the latter.

Angular error versus dynamic control

Dynamic VR analyses showed greater performance when the visuo-oculomotor and vestibular sources of information were available than when they were used in isolation. In the combined condition, VR was maintained to a correct value (between 0.8 and 1) during the whole movements. The hand angular error evolved slowly as the movement unfolded (because of the VR that was slightly <1), but without a sharp variation like that observed in the vestibular and ocular conditions. Nevertheless, after the 60° stimulus displacements, the terminal hand angular errors were not consistently lower in the combined condition than in other conditions. This may suggest that performance optimization, and therefore the finality of the compensatory arm movements during body rotations, consisted in the subjects reproducing the dynamic characteristics of their body motion with their hand and not in controlling the position of the hand in space.

Signals from the semicircular canals are known to convey information about head angular velocity, and ocular muscle proprioception (especially from palisade endings) is known to provide eye motion information in combination with oculomotor efference copy (Donaldson and Knox 1993; Gauthier et al. 1995). It is highly conceivable that the parameter that is primarily used to inform about movement (i.e., velocity) also stands as the primary parameter used to control movement. Controlling the dynamic of the effectors rather than position has also been evidenced in oculomotor studies (e.g., vestibulo-ocular reflex, smooth pursuit; Bahill and Stark 1979; Lisberger et al. 1987; Robinson 1975) and in postural studies (Jeka et al. 2004). Controlling hand motion rather than hand position could also be the goal, for instance, of a waiter who loses balance while holding a tray loaded with glasses. Indeed, presumably, the best way to prevent the glasses from falling in such a situation is to minimize hand acceleration in space, regardless of the initial and final hand positions in space.

Eyes–hand movements: which interaction?

Although it was not the primary object of this study, our results make it possible to look for similarities between arm- and eye-tracking movement control despite several differences between the two systems. The comparison between the eye and arm responses to rotation gains significance, given the divergent opinions on the degree to which eye and arm motor control share similar or interactive processes (for a review see Carey 2000).

In the ocular condition, both the ocular and manual VR values decreased as the frequencies increased during the acceleration phase. During the deceleration phase, ocular and
manual VR values increased with rotation frequency. These effects were the result of lags between stimuli and effectors displacements. Distinguishable effects of rotation frequency, however, were observed on hand- and eye-tracking movements in the combined condition: the frequency effect disappeared for manual tracking, but was reduced only for ocular tracking. The difference in inertia between the arm and the eyes could explain why the rotation frequencies had different effects on the manual and ocular VR values. When the body was rotated, the arm inertia likely facilitated motion of the hand with respect to the trunk. As a result of mechanical properties of the eyes and of the fact that the eyes were nearly aligned with the axis of rotation of the platform, the inertial forces had small effects on the ocular movements. Then, despite facing similar sensorial signals about body rotation, different lags could have been observed between ocular and manual movements because of different inertial properties.

Various studies have shown close links between arm and gaze controls, based on neurophysiological or behavioral observations. The arm movement has been reported to influence the ocular displacements (Fisk and Goodale 1985; Gauthier et al. 1988; Lackner 1975; Nanayakkara and Shadmehr 2003; Neggers and Bekkering 2000; van Donkelaar et al. 2004; Vercher et al. 1996) but the reverse has also been reported (Andersen et al. 1998; Battista et al. 1999; Henriques and Crawford 2002; van Donkelaar 1997b). The fact that the hand movements did not mirror eye movements may also suggest that the arm movements were not exclusively controlled by the oculomotor signals generated during pursuit eye movements. It also suggests that if arm proprioception influenced the eyes, then this influence had only a minor effect on the accuracy of the pursuit eye movements. The contribution of arm muscle proprioception to tracking eye movements would therefore be smaller when the hand is tracking the target, as in the present experiment, than when the arm is used to move the target (Gauthier and Hofferfer 1976; Lackner 1975; Vercher and Gauthier 1992). Therefore the ocular and manual behavior observed in the combined condition of the present experiment provides some support to the segregated controllers hypothesis.

In conclusion, this study showed optimal hand-tracking performance when the visuo-oculomotor and vestibular signals provided information about relative hand–target motion. The use of visuo-oculomotor and vestibular information to control the arm movements during body motion could not be explained by either a unimodal integration model of both sources of signals or by a simple multimodal weighted additive model. The results support a functional model in which vestibular and visual signals or by a simple multimodal weighted additive model. The results support a functional model in which vestibular and visual signals or by a simple multimodal weighted additive model. The results support a functional model in which vestibular and visual signals or by a simple multimodal weighted additive model.

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