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The contribution of otoliths and semicircular canals to the perception of two-dimensional passive whole-body motion in humans

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1. Perception of two-dimensional (2-D) whole-body passive motion in the horizontal plane was studied in twelve blindfolded healthy volunteers: pure rotation in place (180 deg), linear motion (4·5 m) and a semicircular trajectory (radius, 1·5 m; angular acceleration, 0·2 rad s^{-2}) were applied in random sequence by means of a remote-controlled robot equipped with a racing-car seat. The seat orientation in the horizontal plane was controlled by the experimenter, independent of the robot trajectory. Thus different degrees of otolith–canal interaction were obtained. The maximal linear acceleration during the semicircular trajectory was 0·1 *g*; however, the linear acceleration vector was complex as it rotated relative to the subject's head.

2. In the first of two sessions, subjects were instructed to maintain an angular pointer oriented towards a remote (15 m) previously seen target during the passive movements. In the second session they had to make a drawing of the path of the perceived trajectory, after the movement was finished.

3. The results showed that, on average, the movement of the pointer matched the dynamics of the rotatory component of the 2-D motion well. This suggests that, in the range of linear accelerations used in this study, no appreciable influence of otolith input on canal-mediated perception of angular motion occurred.

4. The curvature of the drawn paths was mostly explained by the input to the semicircular canals. Subjects' reconstruction of motion did not account for the directional dynamics of the input to the otoliths occurring during passive motion.

5. This finding proves that reconstructing trajectory in space does not imply a mathematically perfect transformation of the linear and angular motion-related inputs into a Cartesian or polar 2-D representation. Physiological constraints on the interaction between motion direction and change of heading play an important role in motion perception.

The contribution of the vestibular system to the orientation and localization of the body in space during displacements has been suggested by several authors (Worchel, 1952; Barlow, 1964; Beritoff, 1965; Guedry, 1974; Potegal, 1982; Miller, Potegal & Abraham, 1983; Etienne, Maurer, Saucy & Teroni, 1986; Mittelstaedt & Glasauer, 1991; Wiener & Berthoz, 1993). Recent findings have provided further convincing evidence that during rotational (Bloomberg, Melvill Jones & Segal, 1991; Mergner, Siebold, Schweigart & Becker, 1991; Metcalfe & Gresty, 1992; Israël, Sievering & Koenig, 1995) and linear (Israël & Berthoz 1989; Israël, Chapuis, Glasauer, Charade & Berthoz, 1993; Berthoz, Israël, Georges-François, Grasso & Tsuzuku, 1995) whole-body motion along a short path, the brain can provide estimates of the heading direction as well as of the distance solely from inertial information. It has thus been suggested that, besides its functions in regulating and stabilizing gaze, posture and movements, the vestibular system assists in spatial orientation and path integration. Navigation in the absence of external cues can be based either on the inertial signals induced by body movement in space and/or on the sensorimotor signals (proprioceptors in the legs and efference copies of the respective motor commands) concerning body movement relative to the substrate. The effect of the latter information on the orientation during human locomotion has been recently investigated in normal and labyrinthine defective subjects (Bles, Dejong & De Wit, 1984; Mittelstaedt & Glasauer, 1991; Glasauer, Amorim, Vitte & Berthoz, 1994; Gordon, Fletcher, Melvill Jones & Block, 1995; Rieser, Pick, Ashmead & Garing, 1995). The present study is concerned with the ability of human subjects to reconstruct two-dimensional (2-D) motion in the horizontal plane solely from inertial signals.

In humans, linear and angular components of head motion stimulate specific vestibular organ receptors, the otoliths and semicircular canals. Despite some similarity in their functions and the neighbouring anatomical receptor location, the otoliths and semicircular canals represent sensory inputs of different modality: from the mechanical point of view, linear and angular accelerations are independent of each other. Furthermore, the natural reference frame in which such inputs are collected is purely egocentric (the head). However, interpreting whole-body motion requires a dynamic combination of otolith and canal signals and its transformation into a Cartesian allocentric representation. Theoretically, it is possible to reconstruct any complex head motion in the horizontal plane knowing these two inputs. However, little is known about possible interactions between linear and angular components in the perception of 2-D motion (Guedry, 1992; Guedry, Rupert, McGrath & Oman, 1992; Mittelstaedt, 1995; Mittelstaedt & Mittelstaedt, 1996).

Studies of otolith–canal interactions have been mainly concerned with motion perception and lateral eye nystagmus elicited by linear acceleration vectors rotating in the skull X–Y plane (Guedry, 1974; Benson, 1974; Benson, Diaz & Farrugia, 1975; Darlot, Denise, Droulez, Cohen & Berthoz, 1988; Denise, Darlot, Droulez, Cohen & Berthoz, 1988; Mittelstaedt, Glasauer, Gralla & Mittelstaedt, 1989). The findings indicate that linear acceleration can modify, or even produce, reflex eye movements both in the presence and in the absence of canal input. Concerning eye movements, some researchers propose that, in humans, central interactions between linear and angular inputs are only rudimentary (Fetter, Heimberger, Black, Hermann, Sievering & Dichgans, 1996). Moreover, Guedry *et al.* (1992) emphasized that the dynamics of spatial orientation perception could differ substantially from the dynamics of reflex eye movement.

It is known that pure otolith stimulation by a continuously rotating linear acceleration vector produces a variety of perceived movements, including angular rotations, as in off-vertical axis rotation (Guedry, 1974; Benson *et al.* 1975; Denise *et al.* 1988) or in the 'barbecue spit' rotation (Benson & Bodin, 1966; Mittelstaedt *et al.* 1989) or in counter-rotation on a centrifuge (Benson, 1974). However, these findings cannot be compared directly with the situation of the simultaneous transient (not cyclical) stimulation of both otoliths and semicircular canals. In off-vertical axis rotations, the direction of gravity is available as an important directional cue, whereas in our study the low acceleration (0·1 g) yields a resultant with the gravity vector that tilts only about 6 deg with respect to the vertical, which can hardly be noticed. Moreover, recent neurophysiological findings such as those of the head direction cells in the rat (Taube, Muller & Ranck, 1990) and in the primate (E. Rolls, unpublished observation) brain and those of neurones responsive to whole-body translations (O'Mara, Rolls, Berthoz & Kesner, 1994), suggest that representing heading direction in the horizontal plane (orthogonal to the gravity vector) might involve specific processing mechanisms.

The aim of this work was to study the integration of otolith and semicircular canal inputs in the internal model for spatial orientation and motion perception in humans. Subjects were asked to estimate either their body orientation in space (by pointing to a remote memorized target), or body trajectory. We applied several types of 2-D motions to the subject seated on a mobile remote-controlled robot. The seat orientation in the horizontal plane was controlled independently of robot motion, so that different degrees of otolith–canal combined stimulation were obtained. In this way we sought to dissociate the contribution of both sensors to motion perception.

METHODS

Twelve naive volunteers (nine men and three women) with no history of vestibular disease participated in the study. They gave their written, informed consent to the study, which was approved by the local ethics committee. Each subject wore a blindfold and headphones delivering white noise. Subjects were seated on a remote-controlled mobile robot (Berthoz *et al.* 1995) equipped with a racing-car seat (Fig. 1*A*). The head was supported in the roll and yaw planes by soft cushions. The mobile robot (Robuter™; Robosoft, Bayonne, France) was controlled (acceleration, speed, position) by a remote computer via wireless modems. The trajectory followed by the robot was recorded with a precision of 1 mm, at a sampling rate of 25 Hz, by means of optically encoded odometry.

The orientation of the seat in the horizontal plane could be manually controlled, independent of the robot trajectory. The seat was rotated relative to the robot chassis by an experimenter following the robot. The angular motion of the seat relative to the chassis was recorded by means of a potentiometer (at the sampling rate of 25 Hz) and verified after the experiment. The trial was repeated if the control of the seat was inaccurate (deviations from the desired orientation greater than 20 deg). The vertical axis of seat rotation was collinear with the axis of head rotation. Seat orientation in space was computed by subtracting seat orientation relative to the robot from the robot orientation relative to the room.

The following motions were presented in random order to the subject: pure 180 deg rotation in place (condition I); clockwise (CW) semicircular trajectory (Fig. 2*A*; condition II); CW semicircular trajectory while the seat orientation in space was kept constant (Fig. 2*B*; condition III); CW semicircular trajectory, with constant seat orientation during either the acceleration (Fig. 2*C*) or the deceleration phase of robot motion (Fig. 2*D*) (condition IV); counterclockwise (CCW) semicircular trajectory with seat orientation kept constant relative to the direction of the rotating linear acceleration vector (Fig. 2*E*; condition V); linear trajectory with the seat rotating 180 deg to the left during motion (Fig. 2*F*; condition VI).

In all cases, the angular velocity profile of the robot motion was triangular (Fig. 1*C*) and the magnitude of the angular acceleration (and deceleration) was kept approximately constant (0·2 rad s^{-2}). The radius (r) of the semicircular trajectories was always 1·5 m, and the total distance traversed was 4·7 m ($\pi \times 1{\cdot}5$ m). The linear displacement of condition VI (4·5 m) also had a triangular velocity

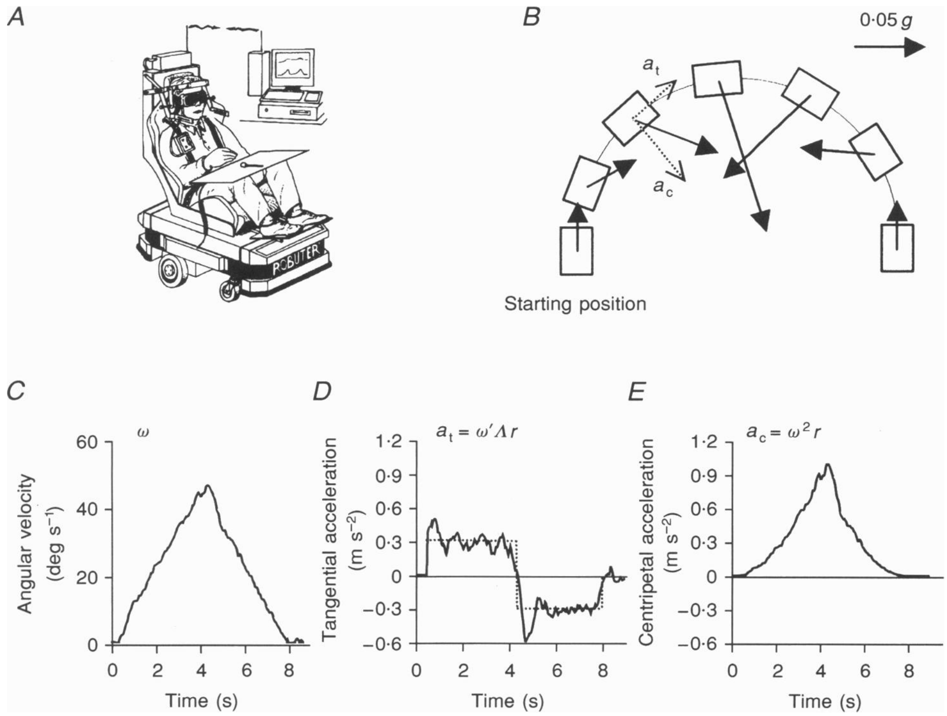

Figure 1. Experimental set-up and characteristics of a semicircular trajectory

A, experimental apparatus with subject; *B*, robot motion and rotation of linear acceleration vector (continuous arrows) during a 180 deg circular arc; the vector scale is at the top right corner; a_t and a_c correspond to the tangential and centripetal components respectively (dotted arrows). From actual experiments, typical traces are shown for angular velocity profile (*C*), tangential acceleration profile (*D*) and centripetal acceleration profile (*E*).

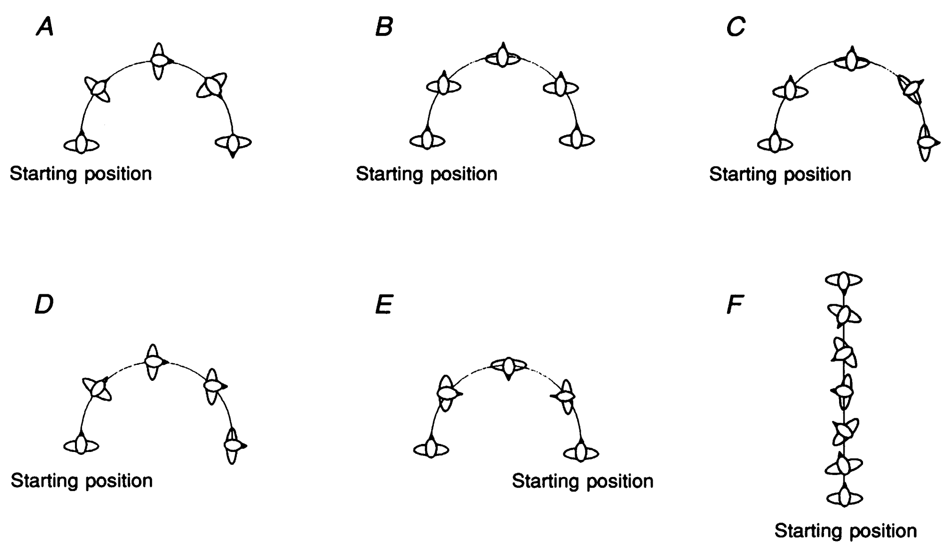

Figure 2. Schematic view of applied trajectories

A, 180 deg arc of circular trajectory (condition II); *B*, semicircular trajectory with stabilization of seat orientation in space (condition III); *C*, semicircular trajectory with stabilization of seat orientation during the acceleration phase of robot motion (condition IV); *D*, semicircular trajectory with stabilization of seat orientation during the deceleration phase of robot motion (condition IV); *E*, semicircular trajectory with stabilization of seat orientation relative to the direction of the rotating linear acceleration vector (condition V); *F*, linear motion with 180 deg seat rotation (condition VI).

profile with an acceleration (and deceleration) of 0·3 m s^{-2}. The duration of motion was the same (about 8 s) in all cases.

The robot design allowed only seat rotation to the left (CCW) relative to the robot chassis. This was the reason why we applied semicircular trajectory to the right (CW) when we stabilized seat orientation in space (Fig. 2*B*, *C* and *D*) and semicircular trajectory to the left when we stabilized seat orientation relative to the rotating linear acceleration vector (Fig. 2*E*).

Properties of a semicircular trajectory

In circular motion the linear (v) and angular (ω) velocity vectors are related to each other by the simple relationship (where Λ denotes vector product):

$$v = \omega \Lambda r,$$

the scalar of radius vector (r) being 1·5 m. After differentiating a linear acceleration vector is obtained:

$$a = (\omega \Lambda r)' = \omega' \Lambda r + \omega \Lambda r' = \omega' \Lambda r + \omega \Lambda v,$$

where $\omega' \Lambda r$ is the tangential acceleration vector (a_t) and $\omega \Lambda v = \omega^2 r$ is the centripetal acceleration vector (a_c). These two components result in a linear acceleration vector whose magnitude and direction change throughout the motion. Since we used a triangular velocity profile, the tangential acceleration was approximately constant and equal to 0·3 m s^{-2} (0·2 rad s^{-2} × 1·5 m; Fig. 1*D*) with a sudden reversal in direction at the velocity peak. On the other hand, the centripetal acceleration changed monotonically during the motion. The actual profile of the tangential and centripetal accelerations is shown in Fig. 1*D* and *E*. The resultant linear acceleration vector rotated relative to the robot (Fig. 1*B*).

The trajectories of conditions II, III, IV, V and VI differed from one another in the magnitude and direction of rotation of the linear acceleration vector relative to the subjects' head. In condition II there was a 180 deg rotation to the right, in condition III a 360 deg rotation to the right, in condition IV a 270 deg rotation to the right, in condition V the subjects' head was stabilized relative to the linear acceleration vector and in condition VI there was a 180 deg rotation to the left.

Experiment A: perception of angular displacements studied by tracking of a remote memorized target

This experiment was designed to investigate the dynamic perception of body orientation in the horizontal plane. The subjects had to maintain a custom designed pointer towards a remote (15 m away, in front of the initial position) previously seen target while being passively displaced ('tracking' task). The pointer was installed onto a square platform maintained on the subject's knees so that he/she could orient it in the horizontal plane. The pointer was coupled to a potentiometer and its movement recorded on the PC in real time at a sampling frequency of 25 Hz. Before the experiment the blindfolded subject was asked to point in different directions (0, 30, 60, 90, 120 deg, etc.) in random order. The preliminary calibration showed that the error in pointing never exceeded 15 deg. The error was very small (never greater than 5 deg) when pointing at 'cardinal' angles (0, 90, 180 and 270 deg).

The small relative translation of the target occurring in the semicircular trajectories was expected to bias the estimation of body rotation by 11 deg (3/15 m corresponds to 0·2 rad).

Each trajectory was applied only once, yielding a total of seven trials. The whole experimental session took about 40 min. The initial position of the robot in the room was always the same. The blindfold was removed before each trial in order to allow a visual exploration of the surroundings. After the trial, the subject, still blindfolded, was slowly (0·09 m s^{-1}, 5 deg s^{-1}) transported back to the initial position. Only then was the blindfold removed so that no correction based on previous error could be made in the following trial.

Experiment B: perception of the trajectory shape

This experiment was performed with the same subjects, after experiment A, in order to appreciate their subjective representation of 2-D passive motion. Subjects were asked to make a drawing of the perceived trajectory immediately after being passively transported. To prevent the subjects from retrieving their actual position in the room, the robot was covered with a thick blanket and the subjects were provided with a light spot. Only then could they remove the blindfolds and make the drawing. In this session only the four trajectories shown in Fig. 2*A*, *B*, *E* and *F* were applied.

Drawings from all subjects were entered into a computer by means of a laser scanner and then superimposed on one another. It should be emphasised that we asked the subjects only to draw the shape of the trajectories without indicating the magnitude of the radius or distance traversed. Therefore the scaling in figures is arbitrary.

RESULTS

Rotation in place (condition I)

Figure 3 illustrates the time course of the average subjects' response during tracking of the remote memorized object during rotation in place. In spite of some inter-individual variability in the perception of angular motion, on average

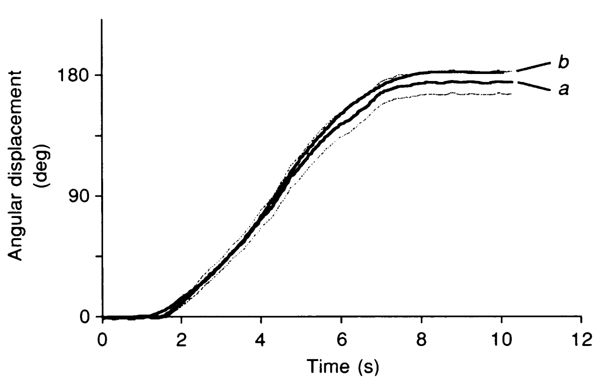

Figure 3. 180 deg rotation in place (condition I)

a, mean (± 1 S.E.M., thin lines) response for all subjects from tracking the remote memorized target during simple rotation in place; *b*, actual seat orientation in space.

subjects were apparently able to estimate in real time their instantaneous orientation relative to the target. The final static angular orientation of the pointer was 173 ± 30 deg to the left (mean ± S.D.) and the range for this measure was 126–223 deg.

The dynamics of tracking movements were, in most cases, proportional to those of the angular motion of the robot: the slope of the instantaneous angle stimulus–response regression line was 1·07 ± 0·24 with $r^2 = 0{\cdot}97 \pm 0{\cdot}02$. The standard error of the estimate (S.E.E.) from the regression line (which quantifies the goodness of response–stimulus matching) was 10 ± 4 deg. The average dynamic response was symmetrical (Fig. 3): the percentage of final response at the instant of the stimulus midpoint (90 deg = 50% of total stimulus) was 49 ± 11%.

Semicircular trajectory (condition II)

During semicircular motion (Fig. 4*A*) the movement of the pointer again matched the dynamics of the angular component of motion (Fig. 4*C*). The final angular position of the pointer was 180 ± 35 deg (mean ± S.D.; range, 130–242 deg). We did not find any appreciable after-effect of rotatory sensation: subjects did not move the pointer after the robot stopped.

The dynamics of tracking movements were again proportional to those of the angular motion of the robot: the slope of the response–stimulus regression line was 1·02 ± 0·22 with $r^2 = 0{\cdot}96 \pm 0{\cdot}03$. S.E.E. was 12 ± 6 deg, which was not significantly different from that of simple rotation in place. We did not find any appreciable delay between pointing movements and the beginning of angular motion, and the responses during the acceleration and deceleration phase were symmetrical: the percentage of total response at the stimulus midpoint was 51 ± 13%, ranging from 27 to 72%. Some subjects showed a larger response during the acceleration phase than during the deceleration phase; other subjects showed an opposite asymmetry; however, on average, the responses during the two phases were symmetrical.

One may wonder whether the inter-individual variability of the final pointing angle can be due to the variability in the dynamic updating of body orientation. The results showed that there was a significant intra-individual correlation between the degree of asymmetry shown in the simple rotation in place (condition I) and in the semicircular trajectory ($r = 0{\cdot}66$, $P = 0{\cdot}02$) but no correlation between the extent of the asymmetry and the final pointing error. It is concluded that the variability in the final angular response probably reflects a specific error in the individual calibration of canal input at the perceptual level and it is not a consequence of distortions in the dynamic response.

The subjective representation of motion in space corresponded to a curved trajectory (Fig. 4*D*). Curvature always displayed the same sign, although there is a considerable degree of variability in the length of the drawn arc. The final perceived motion heading (as it could be retrieved from the drawings) also showed variability corresponding to that of the final pointer position in the tracking task. However, we could not find a significant

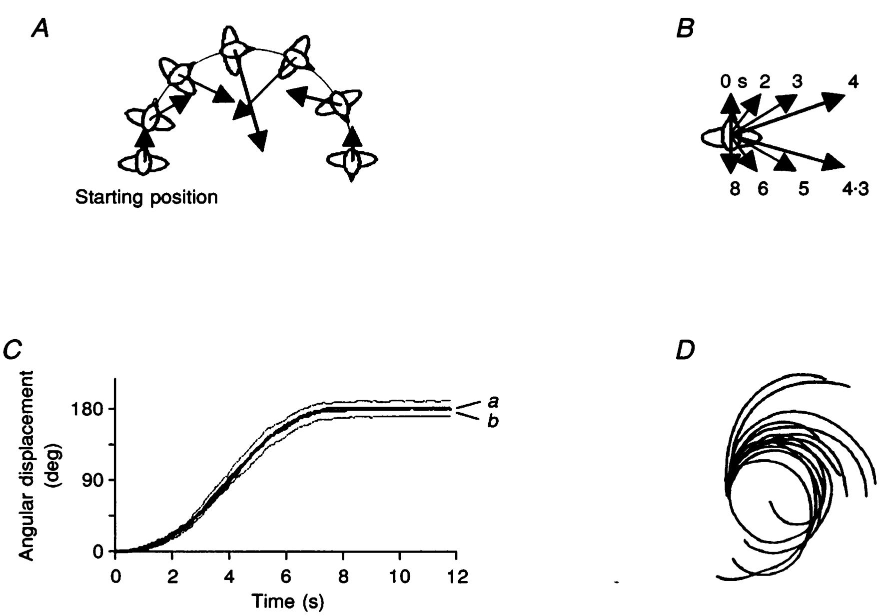

Figure 4. Semicircular motion (condition II)

A, schematic view of the applied trajectory. The evolution of the linear acceleration vector is shown with the arrows. *B*, rotation and change in magnitude of the linear acceleration vector relative to the head (the numbers denote the time from the beginning of motion in seconds). *C*, mean of pointer position responses for all subjects (± 1 S.E.M., thin lines) (*a*) and actual seat orientation in space (*b*). *D*, superimposed drawings by the subjects of the perceived trajectory.

correlation between final motion heading and pointer position.

Stabilization of seat orientation in space during semicircular trajectory (condition III)

Stabilization of seat orientation in space during semicircular robot trajectory was achieved by counter-rotating the seat relative to the robot. The results showed that, on average, subjects rotated the pointer a little to the left. This small response could be due either to the inaccuracy of seat stabilization (Fig. 5*E*) or to the lateral translation of the robot relative to the target. The final angular displacement of the pointer was 15 ± 16 deg (mean ± S.D.), not far from the actual target lateral displacement relative to the initial subject position as shown in Fig. 5*C*. In contrast to condition I, in this condition the linear acceleration vector continuously rotated around the head by 360 deg (Fig. 5*B*).

The subjective representations of motion in space were highly inaccurate (Fig. 5*D*). In the absence of canal stimulation all subjects but one reported a linear motion or a zigzag motion rather than a semicircular one.

Stabilization of seat orientation in space during portions of semicircular trajectory (condition IV)

In most cases, subjects did not rotate the pointer during the portion of trajectory with the stabilized seat (Fig. 6). Yet again, the dynamics of tracking movements paralleled, on average, that of the real angular whole-body displacements. The final pointer orientation during seat stabilization on the first half of robot motion (Fig. 6*A*) was 106 ± 32 deg (mean ± S.D.), and on the second half (Fig. 6*B*) was 100 ± 38 deg (difference between two means was not significant).

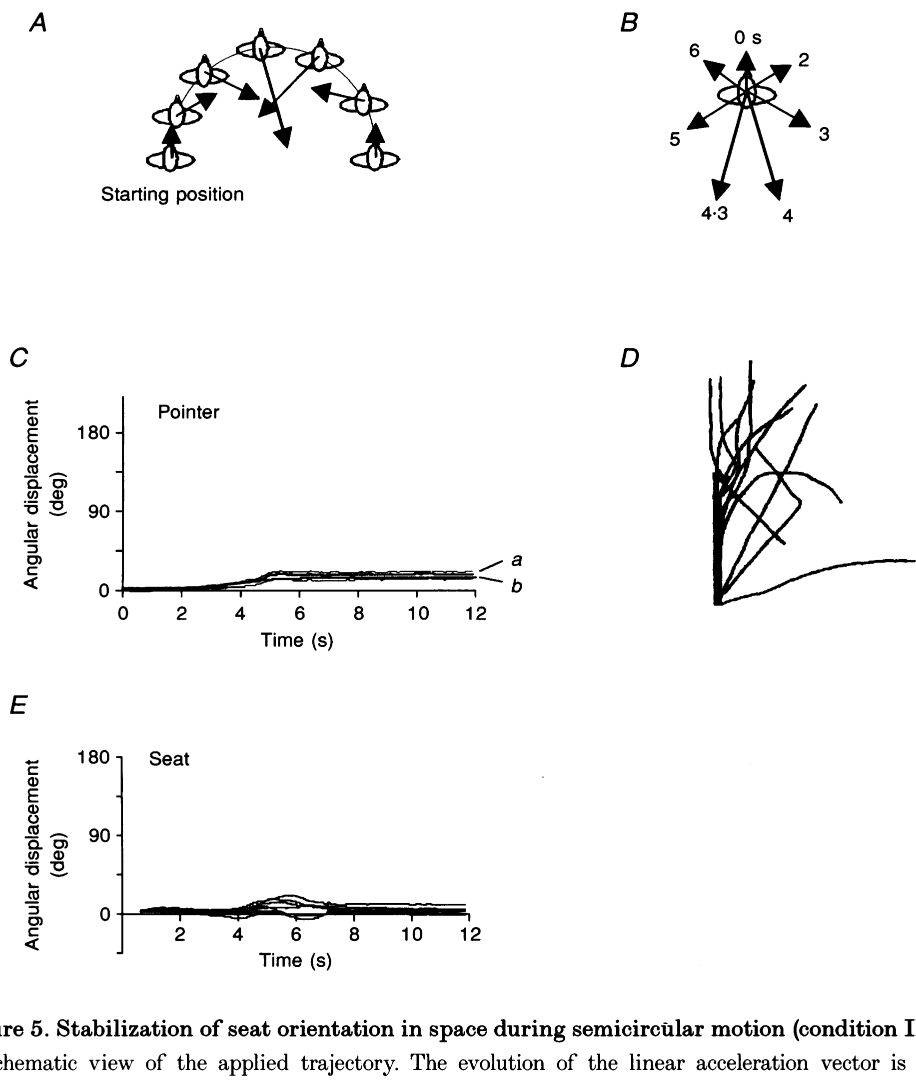

Figure 5. Stabilization of seat orientation in space during semicircular motion (condition III)

A, schematic view of the applied trajectory. The evolution of the linear acceleration vector is shown. *B*, rotation of the linear acceleration vector relative to the head of the subject (the numbers denote the time from the beginning of motion in seconds). *C*, mean subject response (±1 S.E.M.; thin lines) (*a*) and theoretical pointer displacement with translation relative to target taken into account (see text) (*b*). *D*, superimposed drawings by subjects of the perceived trajectory. *E*, stability of seat orientation. Six superimposed curves show the seat orientation in space (obtained by subtracting seat angular position relative to the robot from robot angular position in space).

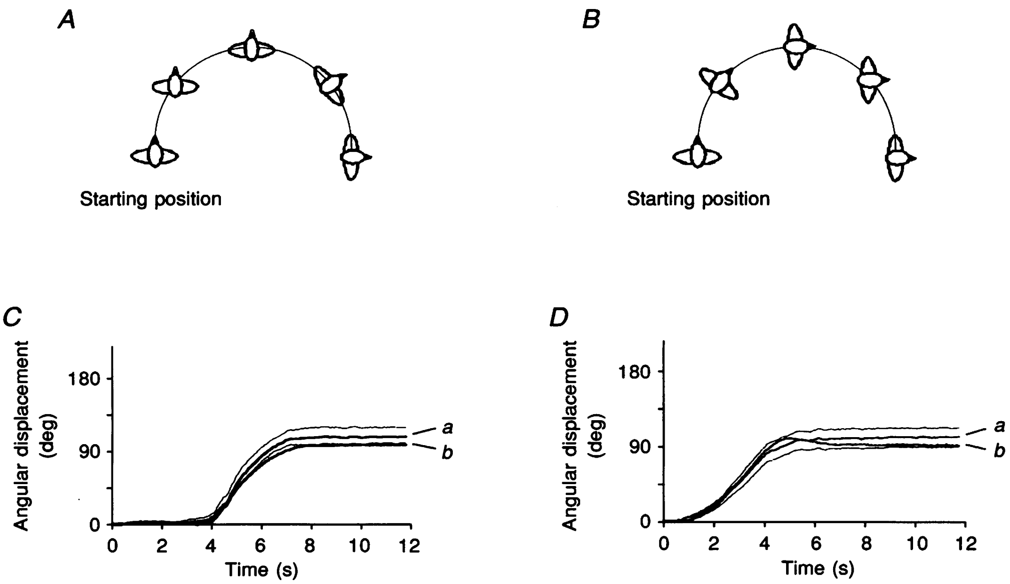

Figure 6. Stabilization of seat orientation during the acceleration (*A*, *C*) and the deceleration (*B*, *D*) phase of semicircular robot motion (two versions of condition IV)

A and *B*, schematic views of the two applied trajectories; *C* and *D*, mean subject response (± 1 S.E.M.; thin lines) (*a*) and actual seat orientation in space (*b*).

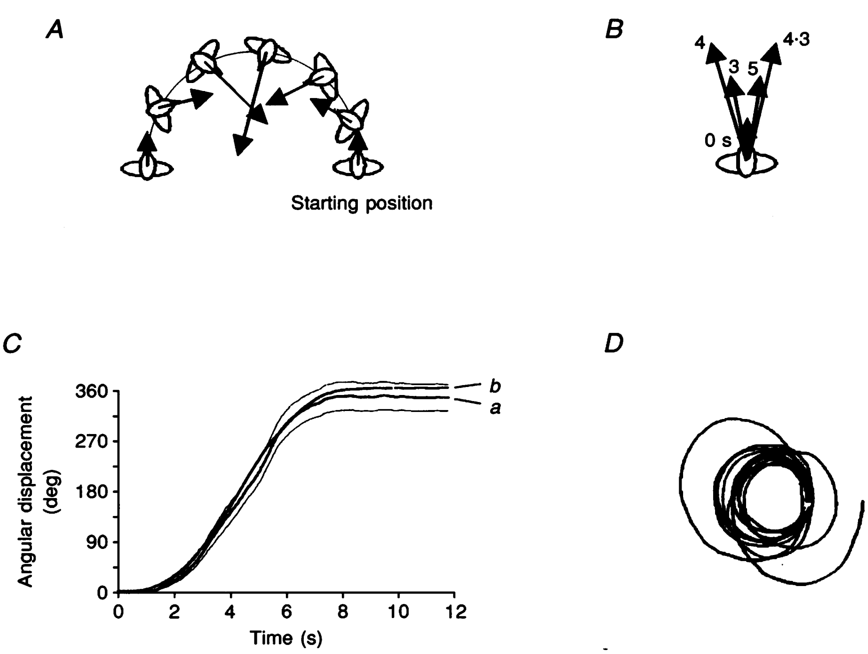

Figure 7. Semicircular motion, stabilization of seat orientation relative to the rotating linear acceleration vector (condition V)

A, schematic view of the applied trajectory. The evolution of the linear acceleration vector is shown. *B*, rotation of the linear acceleration vector relative to the head of the subject (the numbers denote the time from the beginning of motion in seconds). *C*, mean subject response (± 1 S.E.M. ; thin lines) (*a*) and actual seat orientation in space (*b*). *D*, superimposed drawings by subjects of the perceived trajectory.

Semicircular trajectory, stabilization of seat orientation relative to the rotating linear acceleration vector (condition V)

Stabilization of seat orientation relative to the rotating linear acceleration vector required a 180 deg rotation of the seat relative to the robot chassis, in the same direction as the angular robot motion (left). As a result, the real total angular displacement of the subject's head was 360 deg. In fact, the total angular displacement that subjects made with the pointer was 334 ± 73 deg (mean ± S.D.), i.e. close to the applied angular stimulus (Fig. 7*C*).

The subjective representation of motion corresponded, on average, to a full circular trajectory instead of the true semicircular one (Fig. 7*D*). An anecdotal observation is that some subjects commented verbally that the radius of this trajectory was smaller than in other trials (Figs 4*D* and 8*D*). This means that the perceived curvature was greater (curvature = radius^{-1}).

Linear motion with 180 deg seat rotation (condition VI)

In this condition, the mean final angular displacement of the pointer was 173 ± 48 deg (mean ± S.D.), not far from the applied angular stimulus of 180 deg (Fig. 8*C*).

Strikingly, all subjects perceived a curved trajectory instead of the imposed linear one (Fig. 8*D*). In this respect, the linear motion accompanied by seat rotation did not differ from the 'normal' semicircular motion of condition II (Fig. 4*D*), despite the orientation of the linear acceleration vector having a totally different time course. This indicates that the subjects did not take into account the dynamics of the linear acceleration vector relative to the head (Figs 4*B* and 8*B*).

DISCUSSION

In the present study, we investigated separately the perception of body orientation in space and the perception of trajectory curvature during 2-D passive transport in darkness. The results showed that (1) in the range of linear and angular accelerations used in this study, body orientation was well perceived, as revealed by tracking task, regardless of concomitant linear stimuli, and (2) in contrast, the interpretation of the displacement depended on the angular stimulus, yielding in some conditions illusory trajectories.

Perception of angular displacements

The instruction given to the subjects was to track the direction towards a memorized object, situated in the far space, during motion. Therefore tracking consists of transforming the perceived motion kinematics into an adequate motor command for the hand. The dynamic updating of body orientation required by the task belongs to a repertoire of natural behaviours. Tracking self-orientation is known to result in a rather appropriate estimation of changes of body orientation up to 200 deg (for review, see

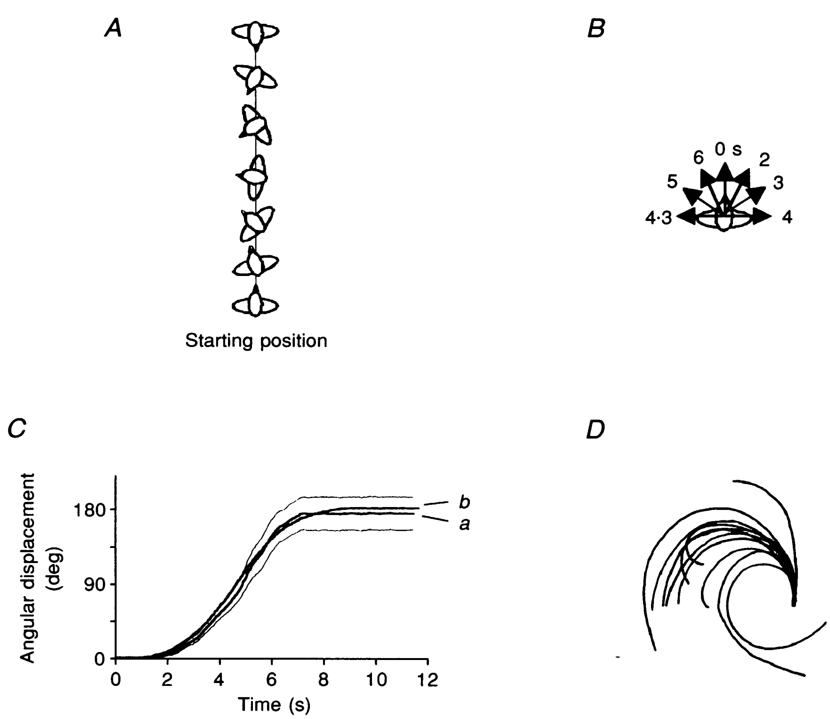

Figure 8. Linear motion with 180 deg seat rotation (condition VI)

A, schematic view of the applied trajectory; *B*, rotation of the linear acceleration vector relative to the head of the subject (the numbers denote the time from the beginning of motion in seconds); *C*, mean subject response (± 1 S.E.M.; thin lines) (*a*) and actual seat orientation in space (*b*); *D*, superimposed drawings by subjects of the perceived trajectory.

Young, 1984). However, by sampling the movement of the pointer during motion we aimed at assessing the accuracy in performing a dynamic updating of body orientation.

In the range of angular velocities used in this study, subjects were able to keep the pointer anchored onto the memorized object during rotation. The inter-individual variability was nevertheless rather large. The movement of the pointer matched well the dynamics of the angular component, both in condition I (rotation in place) and in complex 2-D motion (conditions II–VI), including the conditions in which only part of the trajectory was accompanied by changes in body orientation (condition IV). Therefore, this result provides evidence that humans can estimate in real time their instantaneous angular orientation.

The main finding of this experiment is the observed independence of angular displacement perception upon the concomitant otolith input. Indeed, the different trajectories applied to the subjects had very different dynamics. The linear acceleration vector in the circular trajectory (Fig. 1) not only rotated, but displayed large variations in magnitude in the horizontal plane. However, no systematic effect of the rotation of linear acceleration vector was noted either in the perception of total angular rotation or in the dynamic perception of the instantaneous angle.

Cohen (1977) reported that pilots subjected to centrifugal stimulation in a condition similar to condition V of the present study (180 deg rotation of the centrifuge arm plus 180 deg rotation of the yaw gimbal to keep the subjects aligned with the centrifugal acceleration vector), described an experience of a relatively straight trajectory with a slight skid to the left. Thus in contrast to our results, canal-mediated perception of rotation was largely damped when the direction of the linear acceleration vector was fixed relative to the head. However, the very high value of acceleration (4 *g*) needed to simulate the aircraft catapult launch (which was the context of the study), might have biased yaw perception.

Also, the observed lack of influence of the dynamics of concurrent otolith stimulation on the perception of body orientation is not consistent with what Guedry (1992) reported in subjects undergoing prolonged centrifugation. In this study subjects had to comment verbally, and acceleration (0·33 *g*) and deceleration phases were separated by prolonged (6 min) centrifugation with constant angular velocity. Guedry found a large asymmetry (which could decrease with repetition of trials, see Guedry *et al.* 1992) between angular perception in the initial acceleration and the final deceleration phase of centrifugation: in his hypothesis this depended on whether the linear acceleration vector was rotating in the same direction as that indicated by the semicircular canals or not. Guedry concluded that angular perception strongly depends on the otolith concurrent stimulation. In contrast, we found no difference between the subjects' responses in conditions II and VI, in spite of the fact that the linear acceleration vector was rotating respectively in the same and opposite direction, with respect to that signalled by the semicircular canals.

The reason why we could not reveal an appreciable otolith–canal perceptual interaction might indeed lie in the magnitude of linear accelerations. In our experiment, linear acceleration did not exceed 0·1 *g* (Fig. 1). However, this value is well above the otolith threshold (Gundry, 1978; Benson, Spencer & Stott, 1986) for the detection of the direction of linear movements (about 0·006 *g*). Another explanation for the mentioned discrepancy may lie in the rather 'unnatural' separation of the acceleration and deceleration phases of the quoted study. Physiological movements involve, more typically, rapid acceleration–deceleration cycles and the internal model of motion may include some constraints related to these properties of the stimulus.

By using centripetal accelerations in the same range (up to 0·125 *g*) as in our experiments, Mittelstaedt (1995) and Mittelstaedt & Mittelstaedt (1996) found that the canal-mediated perception of angular motion during long-lasting rotations in a centrifuge decayed more or less rapidly according to the magnitude of the centripetal acceleration vector. However, they pointed out that the perception of angular motion at the beginning of the stimulus was veridical independently of the centripetal acceleration. Hence the otolith–canal interaction they observed seemed to occur only during the stimulus phase at constant angular velocity. Our subjects were submitted to the angular acceleration steps for 8 s and with no constant velocity phase, and the results seem to be consistent with what happened at the beginning of the stimuli of the cited studies. However, additional observations under different conditions are needed to clear up these questions.

Perception of trajectory

The second main finding of the present study is that the interpretation of the displacement depended on the characteristics of the concomitant changes in body orientation, yielding illusory trajectories in conditions III, V and VI, as revealed by the drawing task. Blindfolded subjects had an accurate perception of their 2-D motion only when the orientation of the body was coherent with motion heading (Fig. 4*D*). Otherwise, the perceived curvature accounted mostly for the perception of the motion angular component: approximately linear trajectories were perceived when canal input was absent (Fig. 5*D*), curved trajectories were perceived during linear displacements with simultaneous yaw rotations (Fig. 8*D*) and full circular trajectories were perceived when 360 deg rotations were imposed onto a semicircular arc (Fig. 7*D*).

We emphasized at the beginning of this paper that the otolith and the semicircular canals represent sensory inputs of different modality: from the mechanical point of view, linear and angular accelerations are independent of each other. Theoretically, it is possible to reconstruct any complex head motion in the horizontal plane on the basis of these two inputs. Nevertheless, it is necessary to stress that otoliths measure linear accelerations relative to the head, and not relative to space. Therefore, otolith inputs do not represent X, Y and Z accelerations in an objective reference frame. Theoretically, to reconstruct the trajectory of the body centre of mass in space, the brain should transfer these signals into another system of co-ordinates, which accounts for the head orientation in space (as retrieved from the canal input). Our results suggest that such a complex co-ordinate transformation is unlikely to occur.

In our view, the occurrence of illusory trajectories reflects some fundamental properties of the internal model for motion perception. The results strongly suggest that the brain is unable to process the fine directional dynamics of otolith input to reconstruct motion in space. Even for the pure otolith–somatosensory stimulation in the absence of semicircular canal input in condition III, the subjects perceived linear or zigzag trajectories rather than circular ones. Yet, linear acceleration is included in the internal model of passive transport since no subjects perceived a simple rotation in place: the otolith sensory system participates at least in the detection of the initial direction of 2-D motion (as can be seen in Figs 4*D*, 5*D*, 7*D* and 8*D*). Probably, it also participates in the estimation of total travelled distance.

Perhaps the contributions of otolith signals to motion perception are mainly confined to unidirectional movements. Recent findings (Israël & Berthoz, 1989; Berthoz *et al.* 1995) have indeed confirmed that the otolith input is involved in the perception of unidirectional movements. Also, one of the main functions of otoliths is to trigger postural adjustments opposite to the direction of a perturbation (e.g. in the postural hip-strategy; Horak, Nashner & Diener, 1990). The observed illusions of 2-D trajectories suggest a perceptual predominance of the angular components of sensed motion. Perhaps this finding reflects the greater importance of body orientation with respect to motion direction during natural movements. The participation of canal input in updating the perceived direction of motion can well explain the illusion of a curved trajectory instead of the linear one (Fig. 8*D*) or that of a circular trajectory instead of the semicircular one (Fig. 7*D*) when the seat was rotating on the robot chassis during motion, as if the body orientation coincided with the direction of motion.

Accordingly, subjects were capable of accurately reconstructing 2-D trajectories on the basis of motion dynamics only when changes in motion direction coincided instant-by-instant with changes in body orientation. This suggests that the neural networks involved in processing sensory signals may contain some intrinsic pre-set linked to the internal model of the body attitude relative to motion. Such a pre-set may act as a physiological constraint producing veridical or illusory motion perception depending on whether or not body orientation maintains a stable relation with motion heading (as happens during normal locomotion). It is worth stressing that, when the constraint is violated (conditions V and VI), the rotational component was still well perceived.

In conclusion, the reconstruction of a 2-D trajectory in space does not simply require a mathematically perfect transformation of linear and angular related inputs. When the problem of path integration is considered, motion perception needs to deal with 2-D space. However, extending models for motion perception from 1- to 2-D is generally achieved by implemented simple algebraic equations in a Cartesian reference, as the vector cross-product (Droulez & Darlot, 1989; Merfeld, Young, Oman & Shelhamer, 1993). We suggest that the brain is not reconstructing the imposed trajectory by implementing an analog of such a mathematical operation: rather it solves a simpler special case where a specific stable configuration of body orientation relative to motion heading is maintained.

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