RESEARCH ARTICLE

R. Jürgens · T. Boß · W. Becker

Estimation of self-turning in the dark: comparison between active and passive rotation

Abstract The present work compares passive and active rotations in darkness with the aim of characterizing the contribution of efferent and proprioceptive information to the perception of angular displacement. The perception of angular displacements was measured in 12 naive subjects (Ss), who either stood on a rotating platform (passive mode, P) or actively turned about their vertical axis by stepping around "on the spot" on a stationary platform (active mode, A). Rotations consisted of short acceleration epochs followed by constant velocity periods of 18.5, 37, and 55°/s, with angular displacements ranging from 30° to 810° (presented in a randomized order); in the case of active turning, Ss had learned to approximately produce any of these three velocity levels on command. Ss indicated perceived displacement either verbally (verbal estimation mode, E), or by stopping their rotation when self-displacement appeared to match the magnitude specified by the experimenter (targeting, T). The resulting four conditions (PE, PT, AE, AT) were administered blockwise. In none of the four conditions was there a systematic dependence of perception on turning velocity. Therefore, the results were pooled across velocities, and the Ss' performance was summarized in the form of estimation curves showing median estimates as a function of physical displacement. There were several differences between the passive and active modes: AE- and AT-estimation curves were linear, close to veracity, and fairly similar to each other. In contrast, the PE-curve was curved rightwardly ("saturation"), with small displacements being overestimated and large ones underestimated, whereas the PT-curve was linear and indicated a pronounced overestimation of large displacements. Moreover, both the random and the systematic errors (measures of individual consistency and correctness of individual calibration, respectively) were significantly smaller in the active than in the passive modes. The observed independence of Ss' perception from turning velocity also during passive rotation suggests that the perceptual time constant was significantly longer than 16 s (a value cited as typical for vestibular perception), being possibly "enhanced" by contextual implications and by expectations of the Ss. The clear improvement of perceptual performance in the active mode testifies to the importance of the efferent and proprioceptive signals arising during active motion. On the assumption that these signals are about as "noisy" as the vestibular ones, the smaller errors during active turning could result from their *combination* with the vestibular signal. Alternatively, they could also be intrinsically less noisy than the vestibular signal and simply *replace* the latter during active motion. In the context of these alternatives (which are not exhaustive), the general problem of sensory fusion is discussed, that is, by which mechanisms are signals from different sensory sources combined to obtain a unified representation of the self's orientation.

Introduction

The ability of humans (and animals) to freely move about would be of little advantage, if not a hazard, if it were not complemented by the ability to navigate and orient in space. Many sensory modalities – vision, inertial idiothesis, substratal idiothesis, audition, etc. – contribute to this ability. Current research is still far from understanding how this very disparate information is integrated to create a unitary response to the question "Where am I?"

We note en passant that the biological problem of *analyzing* how evolution has solved this task is paralleled in contemporary robotics by the problem of *synthesizing* algorithms which, on the basis of such diverse sensors as odometers, accelerometers, ultrasound scans, etc., would create a robust unitary representation of the mobile

R. Jürgens · T. Boß · W. Becker (✉)
Sektion Neurophysiologie, Universität Ulm,
Albert-Einstein-Allee 47, D-89081 Ulm, Germany,
e-mail: wolfgang.becker@medizin.uni-ulm.de

agent's current position. Characteristically, a frequently cited work in this field is entitled 'Where am I?' (Borenstein et al. 1996).

In humans, vision (and visual landmarks in particular) undoubtedly play a dominant role in spatial orientation. However, there are many situations where vision alone is either insufficient (e.g., fast turns, jolts) or unavailable (dark). In the dark, human navigation relies foremost on vestibular signals ("inertial idiothesis"; Mittelstaedt and Glasauer 1991), proprioceptive inflow from the locomotor system ("substratal idiothesis"), and motor outflow to the locomotor system (efference copy). The vestibular contribution can be further divided into otolith (linear displacements) and canal (angular displacements) mechanisms. While the contribution of the vestibular system can be isolated by moving Ss passively, proprioception and efference copy must be treated as a compound signal in healthy Ss.

Navigation during *active linear* displacements has been studied, among others, by Elliot (1987), Laurent and Thomson (1988), Rieser et al. (1990), and Glasauer et al. (1994), while Israël et al. (1993, 1997) have considered *passive* displacements. A comparison between passive and active displacements has been given by Mittelstaedt and Glasauer (1991). In contrast, there is little work on *angular* navigation. Whereas many studies have dealt with the perception of passive rotations (for reviews, see Guedry 1974; Young 1981), the use of vestibular cues in *goal-directed* rotations has been studied only recently by Metcalfe and Gresty (1992) and Israël et al. (1996). However, also these latter studies were basically concerned with *passive* movements in which Ss merely exerted control over the driving gear. However, natural navigation always involves *active* locomotion. The perception of self-rotation during, and/or the perceptual after-effects following, active circling have been considered by Correia et al. (1977), Bles (1981), Lackner and DiZio (1988), and Howard et al. (1998). Of these, only Bles compared *active* and *passive* turning in terms of perceived self-rotation; he recorded the mean perceived velocity during a number (*n*) of full turns in subjects who were either passively rotated (*n*=2) or who walked along a circular path guided by a rotating bar (*n*=18), using the same velocity profile in both conditions (5°/s² initial acceleration followed by a 60°/s constant velocity). The single data point in the displacement-velocity space obtained in this way provides little information on how Ss perceive themselves oriented after active and passive rotations of various amplitudes and velocities.

The present study aims at a more systematic comparison of the perceptions of angular self-displacement evoked by passive and by active rotation in the dark. We hypothesized that the inclusion of efferent and proprioceptive information during active turning would improve the accuracy of the perception of displacement and would compensate for the drop of vestibular sensation during long lasting rotations.

Although the circular walking used in the work cited above (Bles 1981; Lackner and DiZio 1988) is a good approximation of the changes in orientation occurring during natural locomotion, we chose circular stepping in place as the active mode of turning. This allowed us to center our Ss on the axis of rotation, an attitude which: (1) minimizes centrifugal forces, and (2) is comparable to the attitude assumed by subjects on a Bárány chair, the condition most widely used in published work on vestibular turning perceptions.

The term navigation is mostly used with the connotation of navigating toward a target, which can be a previously seen one, a remembered one (after a movement away from the target), or one defined by instruction. However, in a more general sense, navigation requires that Ss have a notion of their current orientation and position at any time during a movement. Conceivably, the mental sets corresponding to goal-directed navigation and to maintaining a current account of one's own whereabouts are different. Therefore, we wondered whether Ss would perform differently when they tried to reach a target by means of a self-controlled active or passive turning movement compared with estimating their angular displacement at some arbitrary instant during a non-targeting rotation. By loose analogy to the effect of a mental target upon the vestibulo-ocular reflex (Barr et al. 1976), we hypothesized that the task of achieving a predefined displacement would improve the veracity of Ss' performance in comparison to a standard estimation task. Accordingly, the present report does not only compare the perceptions of angular displacement during active and passive turning, but also investigates whether and how these perceptions vary with and without the task of reaching a "goal".

Material and methods

Subjects

Twelve paid, volunteering undergraduate students, aged 20–30 (seven male, five female), who were free of known neurological diseases, served as subjects (Ss). They gave their informed consent after having learned the general goals and procedures of the experiment, which had been approved by the local ethical committee. In explaining the experiment, care was taken to keep Ss naive to the specific goals of the experiment in order to minimize the risk that their responses would be affected by preconceptions.

Equipment

Ss were either standing or stepping around in an upright position on a turning platform with their feet confined to the center of the platform by means of a protruding rim of 45 cm in diameter. Platform rotations about the vertical axis could be generated by a servo motor under digital control using a PC with D/A and A/D interfaces. Position and velocity feedback from the platform as well as motor signals to it were updated every ms. There were no perceptible vibrations or jolts during rotation. Angular platform position could be controlled with an accuracy of about 2° within a virtually unlimited range (any number of turns); simultaneously, angular velocity could be controlled with an accuracy better than ±1°/s (rms-error). Head position was recorded using a potentiometer mounted above the platform, which was coupled, by means of a flexible yet torsionally rigid hose, to a helmet-like harness worn

Table 1 List of the 46 combinations of angular velocity (*slow*, *medium*, *fast*) and displacement amplitudes (in degrees) used as stimuli in all four experimental conditions (see text for descriptions of conditions). In condition PE, "slow", "medium", and "fast" corresponded to velocities, v_c, of 18.5, 37, and 55°/s, respectively (constant velocity epoch of stimuli). In the other conditions, subjects were trained to approximately achieve these velocities themselves

18.5°/s slow	37°/s medium	55°/s fast
30	60	120
45	75	135
60	105	150
75	135	165
90	165	180
105	210	210
120	300	240
135	450	270
150	600	300
165	750	330
180		360
210		400
240		450
270		540
300		630
330		720
360		810
400		
450		

by the subject. Integrated into the harness also was a wireless headphone delivering a masking noise during rotations and serving verbal communication. Head-to-trunk rotations were minimized by an orthopedic neck collar.

Experimental conditions

All experiments were performed in complete darkness with Ss being deafened by white noise during their turning to exclude visual and auditory cues. There were two modes of turning, *passive* (P) and *active* (A), and two modes of probing the Ss' perceptions of angular displacement, verbal *estimation* upon request (E) or reaching a predefined, desired displacement ("*targeting*", T). The resulting four conditions (PE, PT, AE, AT) were administered block-wise in four separate sessions. Each session lasted about 40 min and consisted of the 46 stimuli (=turnings) listed in Table 1, which occurred in pseudorandom order. As evident from Table 1, there were three different velocity levels (18.5°/s, 37°/s, 55°/s), to which three amplitude ranges (30°–450°, 60°–750°, or 120°–810°) corresponded. The direction of rotation (left, right) also was randomized, with the restriction that the cumulative displacement would not exceed three full turns during a session. The four conditions are now described in more detail:

Condition PE (passive rotation, verbal estimation upon request)

Ss assumed a fixed, upright position on the platform. Stimulation consisted of constant-velocity turnings of the platform flanked by acceleration and deceleration periods of duration T_a and T_d, respectively, yielding an S-shaped temporal profile of angular position (Fig. 1A). The constant velocity (v_c) assumed one of the three levels described above; it was reached by a smooth rise of velocity of the form

$$v(t) = 0.5\, v_c \cdot (1 - \cos\,(\pi \cdot t / T_a)),$$

with T_a being varied in proportion to v_c to achieve the same peak acceleration (40°/s²) in all cases. All rotations were terminated by
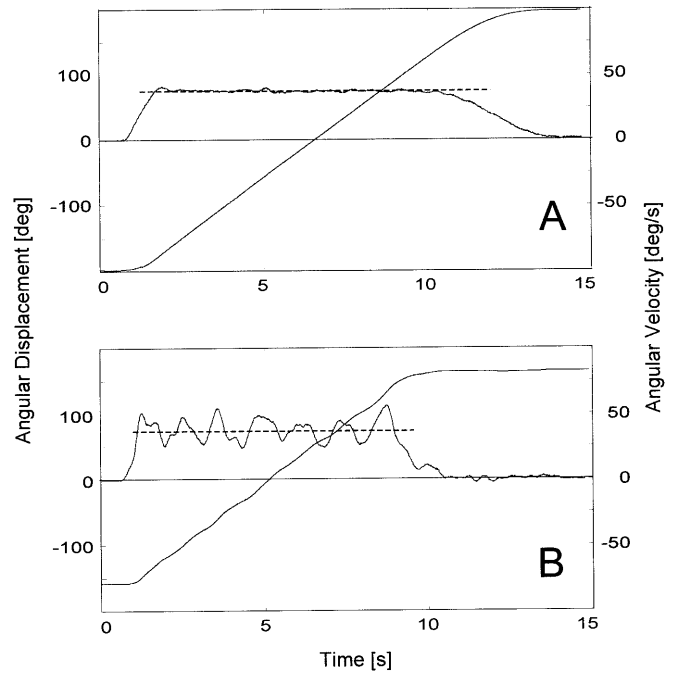

Fig. 1A, B Temporal profiles of head (≈ body) rotation; *solid traces* in each panel show the subject's angular position (*ramp-like curves*) and angular velocity, respectively. **A** Passive condition, paradigm PE; platform is displaced under software control by 400° at a constant velocity of 37°/s with the subject standing motionless on platform; hence, except for a small initial ringing, head rotation is almost identical to platform rotation. **B** Active condition, paradigm AE. Subject turns in small steps on stationary platform at a mean velocity of 36.5°/s (requested velocity was 37°/s); velocity trace is modulated at the pace of the subject's stepping. *Dotted horizontal line* marks mean velocity and time epoch used to calculate it (see text for a description how epoch was determined). In both conditions, when displacement had reached 300°, a request tone was sounded (not shown) instructing the subject to deliver his/her estimate

decelerating the platform along a similar, mirror-reversed time course, but with a peak deceleration of only 13°/s² (i.e., $T_d = 3T_a$). Every turning movement was preceded by a 1000 Hz warning tone of 0.5 s duration. When the angular displacement of the platform had reached a predetermined value (to which we refer below as the stimulus amplitude), a "request tone" (0.2 s, 800 Hz) was sounded, instructing Ss to estimate this displacement. Following the request tone, platform rotation continued for a variable time (typically 0.5 s) before being decelerated and stopped. The stimulus amplitudes were those specified in Table 1. A typical run (one stimulus) from condition PE can be seen in Fig. 1A.

Condition AE (active turning, verbal estimation upon request)

In this condition, Ss were first trained to smoothly step about their vertical axis (i.e., to "turn on the spot") at an approximately constant velocity and, in doing so, to choose among any of three velocity levels approximating the velocities specified in Table 1; for simplicity, these speeds are termed "slow", "medium", and "fast". Ss were free to choose a convenient step-rate/step-magnitude to achieve these velocities. Training was generally completed in about 5 min. In the subsequent experiment, the experimenter first announced the desired velocity and direction of each turning. Then a 0.5 s start signal was sounded, after which Ss were to actively rotate on the stationary platform at the desired speed. As in the passive condition, when their angular displacement (measured

by the head potentiometer) had reached a predetermined value drawn from Table 1 (=stimulus amplitude), a request tone was sounded, instructing Ss to verbally indicate by how much they had turned up to this instant and then to stop their movement. Figure 1B shows a typical example of a subject's performance in condition AE.

Condition PT (passive rotation, targeting)

As in PE, Ss assumed a fixed stance on the turning platform. They could control platform- (and hence body-) turning velocity by manipulating a small spring-loaded lever coupled to a potentiometer which was mounted on a light-weight box suspended from a neck belt. In a brief training session (5 min), Ss learned to smoothly control the platform's turning velocity and to approximate any of the three velocity levels (18.5°/s, 37°/s, 55°/s); to make Ss confident of their control of the platform, they were first given free vision of the laboratory environment before continuing their training in the dark. During the experiment itself, the desired speed, direction, and displacement was verbally communicated before each run (for example: "...next move to the right, medium velocity, amplitude 210°"); the combinations of velocity and amplitude were again drawn from Table 1. Thereafter, the start tone was sounded (same as in PE), and Ss were to rotate themselves by means of the platform at the indicated velocity until they thought they had reached the desired displacement. Thus, instead of verbally estimating their actual displacement as in PE, they controlled their displacement in such way as to match their perception of it to a given value.

Condition AT (active turning, targeting)

As in condition AE, Ss were to actively turn about their vertical axis on the stationary platform. Similar to condition PT, before each run, the experimenter announced the desired velocity, direction, and angular displacement to be achieved by the subject. After the start tone, Ss were then to step around at the indicated velocity until they felt they had reached the desired displacement.

Order of administration

The four conditions were performed on two different days. On the first day, conditions PE and AE were tested, on the second day AT and PT. This fixed order was chosen because, in conditions AT and PT, Ss received explicit information about the magnitudes of displacement and their spacing; we wanted to avoid the transfer of this information to conditions PE and AE. However, within days, the order of conditions was systematically varied. Between the two sessions of a day, there was a pause of 15–20 min, during which the Ss left the laboratory and walked about.

In order to prevent subjects from learning the sequence of stimuli, the stimulus material of Table 1 was arranged into four different pseudorandom lists, which were distributed among Ss and experimental conditions in a balanced way. However, the first stimulus of each session always had a velocity of 18.5°/s and an amplitude of 210° or less. Between successive stimuli, there was a pause of varying duration, depending on the duration of the preceding stimulus ($\approx 1.5 \cdot$stimulus duration, but never less than 20 s).

Specific instructions

We instructed the Ss to view "their nose as a pointer sweeping across the horizon" and to mentally track its motion so as to keep a current record of the ongoing angular displacement. Displacement amplitudes were estimated (conditions PE, AE) or specified (PT, AT), at the Ss' choice either in degrees, using a clock scheme, or as multiples and fractions of full turns. Any meaningful combi-

nation of these systems was also accepted (e.g. "two full turns minus 60 degrees"); in this way, we hoped to reduce the risk that Ss' attention would be diverted from their turning sensations by tedious scale conversions. Preceding each start tone, Ss were verbally warned and asked to concentrate on the imminent rotation. Ss received no feedback whatsoever regarding their performance until the end of the second day, when the whole experiment was completed.

With the estimation tasks PE and AE (first day), Ss were given no explicit information about the stimulus characteristics, but were merely told that some displacements might be significantly larger than one full turn. Ss were to make up their estimates when the request tone was sounded, but to report them only after the masking noise was silenced, indicating the end of the movement.

In the active-movement conditions (AE, AT), Ss were told that there was no need to react as quickly as possible to the start signal; instead, they were to concentrate on keeping track of their movement from its very beginning. Maintaining the requested velocity was depicted as a goal secondary to the task of estimating the angular displacement (or achieving the desired displacement).

In conditions with a verbal estimation task (PE, AE), Ss were instructed to not allow any sensations posterior to the request tone to modify their estimates. In targeting conditions (PT, AT), Ss were asked to try and reach the desired displacement by means of a single, continuous movement. However, when they felt that this movement had not the desired magnitude, they were to correct it by a second move. Also, they were warned not to be misled by any sensation that might arise during or after their deliberate stopping.

At the end of the two sessions of a day, Ss were asked to report their personal observations regarding the quality of their turning sensations, possible after-effects, particular strategies used for estimating, and also to compare the subjective difficulty of the estimation or targeting task across the two conditions.

Data acquisition

Ss' verbal responses (conditions PE, AE) were entered manually into the computer that controlled the experiment. In all conditions, the angular positions and velocities of the platform and the head were continuously digitized at rate of 100 Hz and stored in computer files together with identification codes for later analysis.

Results

Subjective difficulty of the conditions

After the two estimation tasks of the first day (conditions PE and AE), seven of 11 Ss felt that estimation was more difficult during the active condition AE than during the passive condition PE. Some of them thought this difference occurred because their attention was absorbed by the task of maintaining the requested speed of self-turning (although they had received the instruction that speed control was only of secondary importance). Three Ss considered the passive condition more difficult, and one S experienced no difference. Seven Ss were asked whether, in retrospect, they thought that the angular velocity in condition PE had been constant or whether it had diminished in the course of the movements (the importance of this question became only clear in the course of experimentation; therefore, we do not have responses from all Ss). Only one S indicated that turning velocity had faded, whereas the other six Ss thought that it had been constant.
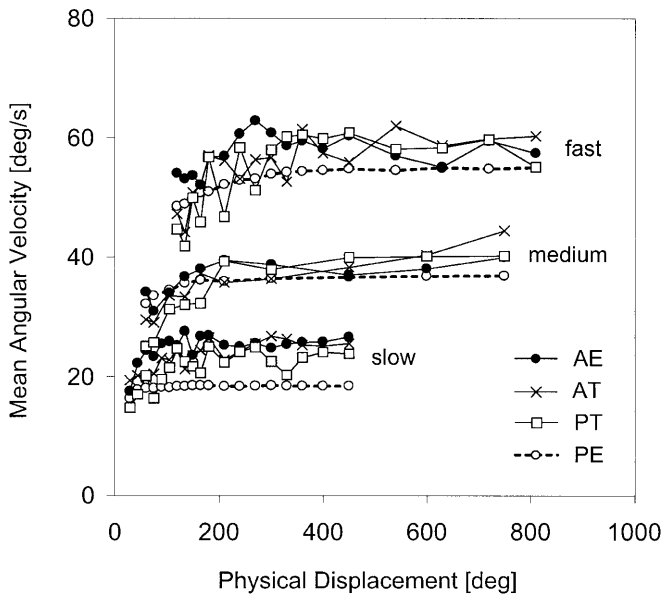
Fig. 2 Mean angular velocity of head (≈ body) as a function of displacement amplitude; median values across subjects. Determination of mean velocity as described in Results and illustrated in Fig. 1B. *Solid curves* Velocities generated by subjects themselves (conditions AE, AT, PT); note segregation into three distinct clusters according to instructions "fast", "medium", and "slow". *Dashed curves* Computer-generated velocities (condition PE). See text for description of conditions

Table 2 Grand averages (*AVG*) and standard deviations (*STDEV*) across subjects of the mean velocities achieved with *Slow*, *Medium*, and *Fast* stimuli (°/s). Velocity means determined as described in Results. Grand averages taken after *within*-subject averaging across all stimuli of a velocity class. *PE*, *PT*, *AE*, *AT* Experimental conditions (see text for descriptions)

		PE	PT	AE	AT
Slow	AVG	18.2	21.5	24.7	23.5
	STDEV	0.2	4.1	6.0	5.4
Medium	AVG	35.4	34.3	36.7	35.7
	STDEV	0.5	5.3	6.9	6.5
Fast	AVG	52.8	55.0	57.5	55.0
	STDEV	0.6	6.8	10.5	7.2

On the second day, after completing the two targeting conditions, all Ss indicated that targeting was more difficult in the passive condition PT (where they had to control platform rotation by means of a lever) than in the active turning condition, AT.

Not unexpectedly, for the passive conditions (PE, PT), all Ss reported a mild post-rotational turning sensation in the opposite direction, which never was nauseous; in this context, it is important to recall that Ss had to make their estimates before the rotation stopped (PE) or to stop it when they thought they had reached the prescribed displacement (PT), and that they were to ignore after-sensations. Finally, no consistent post-rotational sensations were experienced after active turning.

Velocity of self-generated active (AE, AT) and passive (PT) rotations

As shown in Fig. 1B, Ss were able to circle in a relatively smooth way on the stationary platform by stepping around "in place", in spite of an unavoidable modulation of instantaneous angular velocity at the pace of stepping.

To characterize Ss' turning velocity in any of the four conditions, we first smoothed the velocity profiles by means of a moving average window (width 1 s); we then determined the instants where the smoothed velocity first reached half its maximum value and where it last fell below this value. Finally, we calculated the mean of the original (non-smoothed) velocity across the period de-

fined by these instants. In all conditions requiring self-generated stimuli, Ss were able to adjust three clearly distinct, mean velocity levels in response to the commands of the experimenter. This is shown in Fig. 2 (solid curves), which plots the averages of these velocities across subjects as a function of stimulus magnitude. For each condition, three curves are depicted, which correspond, from top to bottom, to the commands "fast", "medium", and "slow". Ss' mean, self-generated turning speeds were fairly constant across the entire range of stimuli, with the exception of turns of 150° or less. For these small turns, the time spent in acceleration and deceleration made up a significant proportion of the total turning time; hence, their mean velocity dropped. Obviously, the same effect also held for the mean velocities to which Ss were exposed in the computer-controlled condition PE (dotted curves in Fig. 2); only with turns of long duration did these mean velocities approach the "nominal" levels of 18.5, 37, and 55°/s.

The mean velocities achieved with the "fast", "medium", and "slow" stimuli are summarized in Table 2 (grand averages across Ss; mean velocities first averaged across all displacement magnitudes within Ss). As can be seen from Fig. 2 and Table 2, Ss' self-generated velocities in response to the "fast" and "medium" commands approximated the desired velocities (i.e., those adjusted in condition PE) fairly well, whereas they were larger with the "slow" command. Although the latter differences were statistically significant ($P<0.05$), the magnitude of these differences still warrants a *common* categorization of the velocities from all conditions into three classes according to the instructions given. As evident from Fig. 2, this was particularly true for large displacements, where the distinction of different velocity levels became important because of the correspondingly different stimulus durations (cf. Discussion).

Displacement estimations

General remarks

The results obtained in a representative sample subject are shown in Fig. 3; each panel in this figure plots esti-

Fig. 3 Displacement estimates obtained in a sample subject (no. 7 in Table 3). Estimates are plotted as a function of the physical displacement (=stimulus). Each data point represents one estimate; *symbols* distinguish the three velocity levels. *Upper panels* Passive conditions PE and PT, *lower panels* active conditions AE and AT. *Panels on the left* show verbal estimations delivered at the sounding of a request signal. *Panels on the right* show targeting conditions with requested displacement (angular target distance prescribed to subject before start of movement) plotted on *ordinate* and displacement actually realized by subject plotted on the *abscissa*; note that the requested displacement magnitude is supposed to equal the subject's estimate of the physical displacement achieved by the time she stops her movement. Estimates on *dashed diagonal line* are veridical
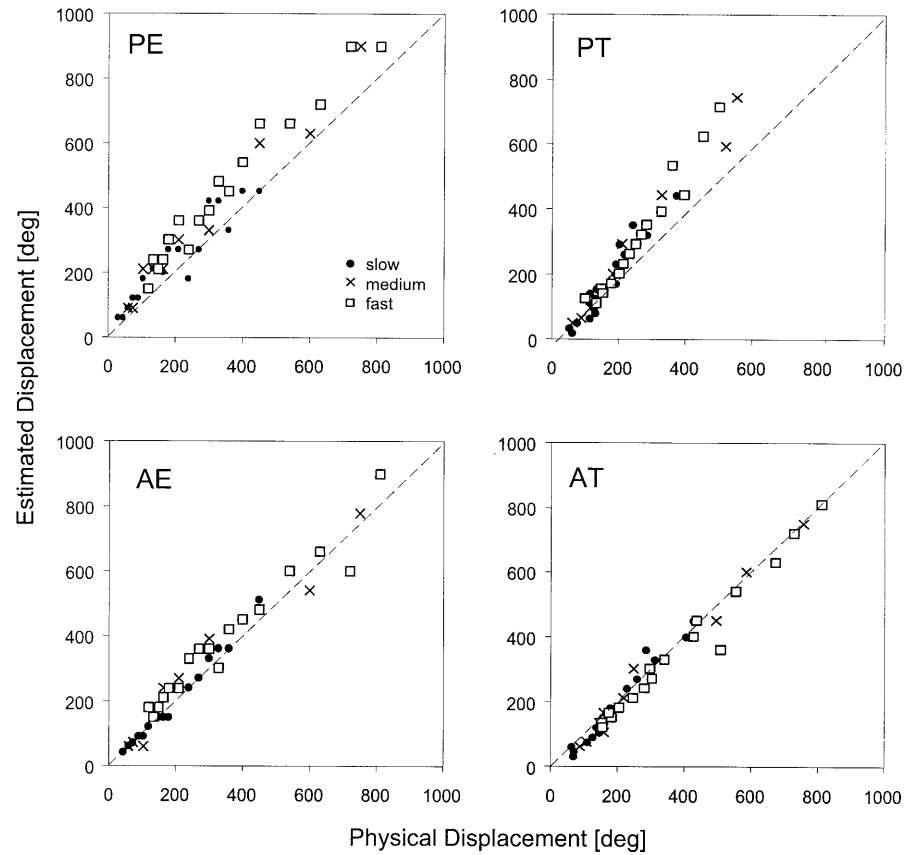

Table 3 Slopes of the linear regressions of estimated versus physical displacement (=stimulus magnitude). The regressions were calculate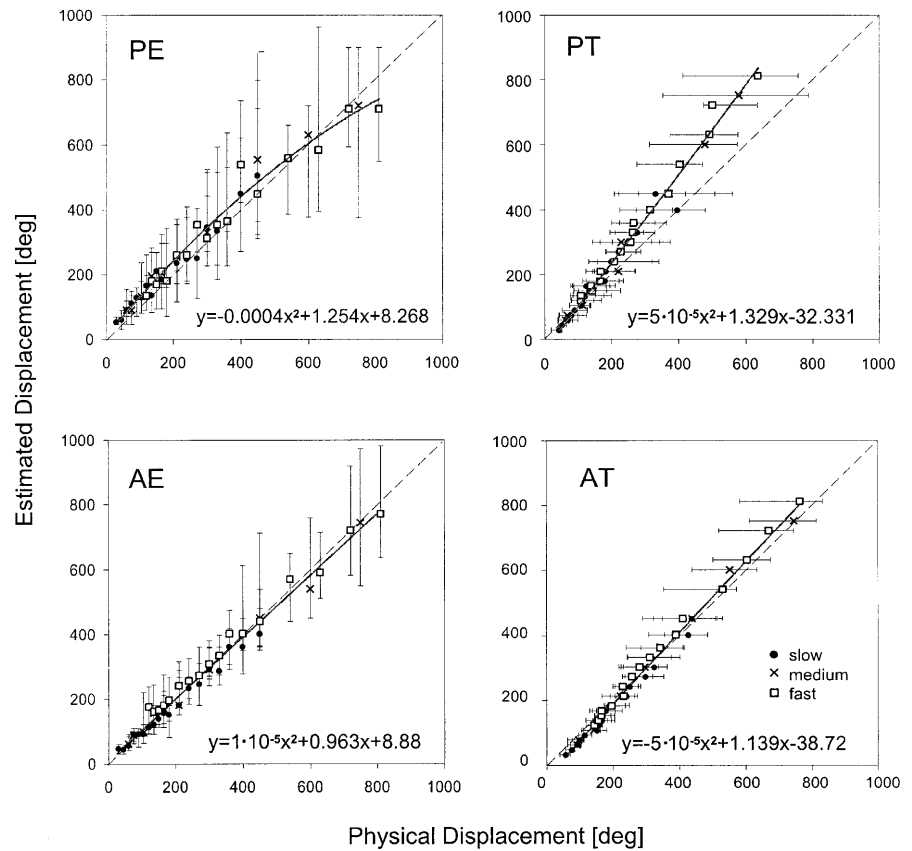d separately for the three turning velocities, *Slow*, *Medium*, and *Fast*, and were restricted to the stimulus range ≤450°. *PE, PT, AE, AT* Experimental conditions (see text for descriptions)

Subject	PE			PT			AE			AT		
	Slow	Medium	Fast	Slow	Medium	Fast	Slow	Medium	Fast	Slow	Medium	Fast
1	1.12	0.75	0.84	1.14	1.60	1.12	1.28	1.15	0.67	1.06	1.08	1.11
2	1.38	0.97	0.95	1.61	1.33	1.44	0.92	0.82	0.75	1.10	1.09	0.96
3	0.76	1.00	1.01	1.04	1.08	1.20	1.02	1.01	1.24	0.99	1.12	1.30
4	0.91	1.09	0.94	0.92	0.94	1.11	1.13	0.90	1.00	1.07	1.19	1.13
5	0.65	1.23	1.46	0.84	0.97	0.67	1.12	0.93	1.05	1.39	1.64	2.04
6	1.08	1.23	1.08	1.62	1.86	1.71	0.81	1.06	0.84	0.99	1.04	0.91
7	0.96	1.21	1.31	1.38	1.49	1.25	1.13	1.16	0.98	1.15	0.98	0.87
8	1.14	1.31	1.11	0.71	0.89	1.23	0.88	0.97	0.86	0.97	0.85	1.00
9	0.42	0.44	0.64	0.88	0.72	0.78	0.69	0.30	0.48	0.76	0.88	0.89
10	1.04	0.83	1.29	1.16	1.02	1.40	0.82	0.83	0.86	0.94	0.90	0.99
11	1.71	1.25	1.09	1.36	1.03	1.09	0.64	0.72	0.87	0.84	1.36	1.31
12	3.37	2.09	1.69	2.14	2.40	1.98	1.54	1.02	1.44	1.61	1.32	1.35
Median	1.08	1.12	1.09	1.16	1.08	1.23	1.00	0.93	0.87	1.06	1.09	1.11

mated displacements as a function of stimulus magnitude, that is, physical displacement, with symbols discriminating "slow", "medium", and "fast" turning velocities. To quantitatively characterize the performance of individual subjects, linear regressions of estimated versus physical displacement were calculated; these regressions were restricted to stimuli ≤450° because only this range was covered by all three turning velocities (450° was the maximum displacement reached by the "slow"

stimuli) and because, within this range, the responses from any of the four conditions (PE, AE, PT, AT) could be reasonably approximated by linear fits. The slopes obtained with this regression analysis are listed in Table 3. Since these parameters were not normally distributed, we used non-parametric methods to test for significant differences (Friedman's ANOVA, Wilcoxon's test of paired matched samples).

Fig. 4 Median values of displacement estimates from 12 subjects. Same format as Fig. 3. *Vertical bars* in PE and AE show the 10%–90% percentiles of individual estimates ("80%-range"). *Horizontal bars* in PT and AT give 80%-ranges of the individual displacements generated by the subjects (*abscissae*) in response to the requested displacements (*ordinates*). *Bold curves* show fits of the median estimate versus stimulus relationships by second-order polynomials (equations in *lower part of panels*; data corresponding to the three velocity levels pooled). See text for description of conditions

PE $y=-0.0004x^2+1.254x+8.268$

PT $y=5\cdot10^{-5}x^2+1.329x-32.331$

AE $y=1\cdot10^{-5}x^2+0.963x+8.88$

AT $y=-5\cdot10^{-5}x^2+1.139x-38.72$

- slow
× medium
□ fast

Estimated Displacement [deg]

Physical Displacement [deg]

The results from all 12 Ss are summarised in Fig. 4, which plots the median values of their estimates (the median was chosen because the individual estimates were not normally distributed). To also provide a global description of our Ss' performance without the above restriction to displacements of 450° and less, second order polynomials were fitted to these medians, pooling all data indiscriminate of turning velocity.

In the following, we shall first describe our Ss' estimation performance separately for each of the four experimental conditions and, then, make comparisons between conditions in terms of the estimation errors.

Verbal estimation of angular displacement: pure vestibular stimulation (condition PE)

Figure 3PE depicts the results of our sample subject (no. 7 in Table 3). The graph plots the angular displacements estimated as a function of stimulus magnitude, i.e., the physical displacement reached at the time the request tone was sounded. Each data point represents one verbally communicated estimate. Several points can be noticed from Fig. 3PE: (1) most stimuli were overestimated (points above diagonal line); (2) estimates appeared to increase linearly with stimulus magnitude; and (3) there was no obvious dependence on stimulus velocity; at best, there was a tendency for low-velocity stimuli (18.5°/s, filled circles) to engender smaller estimates than the other two velocity levels.

Most observations made from the individual example in Fig. 3PE were confirmed by the median estimates from all 12 Ss shown in Fig. 4PE. Estimates did not depend in any systematic way on stimulus velocity (intercepts and slopes tested by Friedman's ANOVA with levels "slow", "medium", "fast"), although, in some individuals, estimates either seemed to increase (e.g., subject no. 5, see Table 3) or decrease with velocity (e.g., no. 11). Because velocity was not a systematic factor, all median data were pooled and fitted by a second-order polynomial (bold curve). The linear term of this fit (1.25) indicates that "small" displacements (up to 450°) were indeed overestimated. However, the quadratic term of the fit, which is negative and significantly different from zero ($P<0.05$), indicates a rightward curvature ("saturation"), reflecting a consistent tendency of our population of Ss as a whole to increasingly underestimate large displacements (different from the sample subject who exhibited an apparently linear relationship).

As a measure of interindividual scatter, the vertical bars in Fig. 4PE show the 10–90% percentile range of the individual data (henceforth called the 80%-range); this scatter was quite large. Therefore, although our Ss' median performance was close to veracity (dashed diagonal line), the mean of the absolute (non-signed) error across Ss (also called "modulus mean error", Poulton 1981; see definition in Fig. 5A) reached substantial values (Fig. 5A, open circles). For example, while Fig. 4PE suggests that displacements of 600° were correctly esti-

mated by our population of Ss as a whole (average signed error close to zero), Fig. 5A indicates that the individual estimates were, on average, about 150° too large or too small. Figure 5A also reveals an interesting anchor effect: the plot of absolute error versus stimulus amplitude (physical displacement) for condition PE (open circles) exhibits local minima for displacements of $n \times 180°$ (n=1, 2, 3, ...), suggesting that half turns and multiples thereof are particularly easy to estimate and/or that a neighborhood of these amplitudes (e.g. 330°–400°) is preferentially expressed in terms of these "natural raster" values. Except for this local modulation, the absolute error exhibits a roughly linear increase with stimulus magnitude when displacements of up to 450° were estimated (slope ~33%).

Verbal estimation of angular displacement: active turning (condition AE)

Figure 3AE shows the verbal displacement estimates of our illustrative subject during the active turning condition, and Fig. 4AE plots the corresponding median values from all Ss. Both figures suggest that the estimates were a linear and highly veridical function of stimulus magnitude. Friedman's ANOVA indicates that turning speed was a significant factor ($P<0.05$). Indeed, although the slopes of estimated versus physical displacement were similar with all velocities, the intercepts of the linear fits differed, the estimates of "slow" displacements being about 40° smaller than those obtained with "fast" ones. However, because this difference is small in relation to the investigated range of displacements, we chose to ignore it in order to obtain a global description of our Ss' behavior and again fitted all data by a second-order polynomial (bold curve). This fit confirms the linearity (non-significant quadratic term) and the veracity of the estimates (linear term of 0.96, i.e., close to unity).

A different picture again emerges if the mean absolute error is considered (Fig. 5A, filled circles). This error, which increased linearly with stimulus magnitude at a rate of about 14%, averaged more than 100° when Ss estimated displacements of 720° or larger, whereas the median error depicted in Fig. 4AE does not exceed 30°. Clearly, however, the absolute errors made during active turning were conspicuously smaller than those observed during passive turning (compare curves PE and AE in Fig. 5A). Finally, as indicated by the smaller 80%-ranges in panel AE of Fig. 4 compared with panel PE, there was also less interindividual scatter with active turning than with purely passive rotations.

Estimation of displacement by targeting: passive rotations (condition PT)

Figure 3PT shows the relationship between the requested displacements and the displacement produced by our sample subject when she controlled platform rotation by
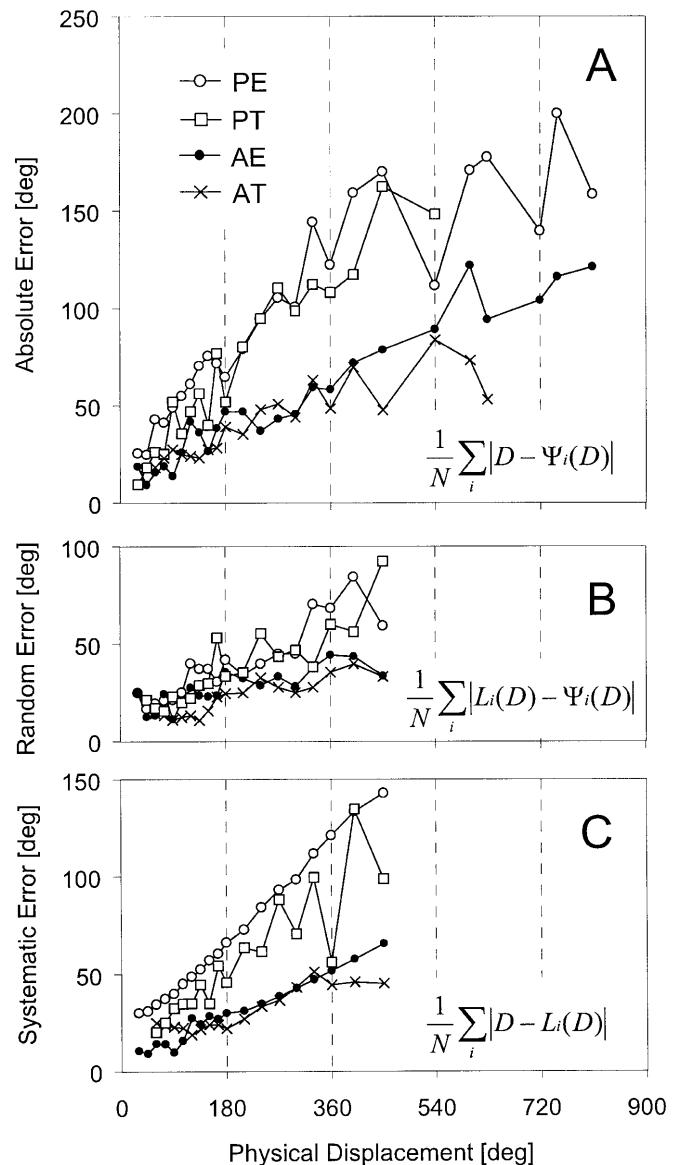

Fig. 5A–C Mean of individual estimation errors as a function of stimulus magnitude (physical displacement, D) in the four experimental conditions (for descriptions, see text). **A** Absolute error (non-signed error; for definition, see formula in *right lower part* of panel). Note local minima of error for integer multiples of 180° (marked by *vertical dashed lines*) in condition PE (*open circles*). **B** Mean random error (consistency of the individual subjects' responses, see formula for definition). **C** Mean systematic error (error of individual calibrations, see formula for definition). N Number of subjects, $\Psi_i(D)$ displacement estimate of i-th individual, $L_i(D)=a_i+b_i \cdot D$, linear fit of $\Psi_i(D)$ in the range $D \leq 450°$. Note that curves from targeting conditions (e.g., curve PT in **C**) have "rugged" behavior because each subject produced a different set of displacements. Hence, mean-error curves for PT and AT were obtained by: (1) sorting the displacements into bins with borders placed midway between successive standard stimulus magnitudes (as listed in Table 1), and (2) attributing the error measures calculated for an individual displacement to the standard magnitude enclosed by the corresponding bin. Thus, if not all subjects generated a displacement in the range of, e.g., 345°–380° enclosing the standard magnitude 360°, the mean error calculated for 360° was based on less than 12 subjects

means of a lever. Here, the requested displacement has been plotted on the ordinate because, by virtue of the instruction given, it equals the subject's estimate of the displacement accumulated up to the moment when she stopped the platform; this displacement represents the physical stimulus and is plotted on the abscissa. The subject mostly stopped the rotation short of the requested angle (data points above dashed line), that is, she overestimated her physical displacements.

Of our 12 Ss, six always produced their displacements in a single move, never making a correction. The other six Ss made a total of 28 corrections (all but one increasing the displacement), with two of these Ss accounting for ten corrections each (mean sizes: 4 and 6%, mean latencies: 810 and 720 ms, respectively). The median displacement results (including corrective movements) from all 12 Ss are shown in Fig. 4PT. Note that, here, the 80%-ranges are plotted horizontally because, as explained above, the Ss' operant responses were the magnitudes of the physical displacements they achieved by lever control. Rotation velocity was not a significant factor (Friedman's ANOVA). Therefore all data were again pooled and fitted by a second-order polynomial (bold curve). It suggests an essentially linear relationship between estimated and actual displacements (non-significant quadratic term), but also a substantial overestimation by about 33%.

The mean absolute errors (Fig. 5A, open squares) were indistinguishable from those observed during passive rotation without targeting (PE), increasing at a rate of about 31% with stimulus magnitude. Finally, we note that, owing to their tendency to fall short of the requested displacements, a number of Ss produced no large stimuli (i.e., no large abscissa values); hence, the plot of absolute error versus displacement was not extended beyond 540°.

Estimation of displacement by targeting:
active rotations (condition AT)

The performance of our illustrative subject is shown in Fig. 3AT, and the corresponding median data representing all 12 Ss are depicted in Fig. 4AT. Note that, similar to Figs. 3PT and 4PT, the abscissa gives the angle by which Ss displaced themselves, while the ordinate shows the requested displacement. Turning speed had no influence on the results, so that all data could be pooled irrespective of velocity. The polynomial fit (bold curve) of the pooled median values suggests a linear (non-significant quadratic term) and almost veridical relationship between the Ss' actual angular displacements and their estimates; when large displacements were requested, Ss stopped short of the desired angle by about 6% (i.e., they overestimated by about 6%), whereas they overshot the smallest requested displacement (30°) by about 18° (equivalent to a 36% underestimation of self-displacement).

The mean absolute error of Ss' estimates during targeting (Fig. 5A, crosses) was much the same as observed in the non-targeting condition AE (filled circles), except possibly for smaller values with displacements of 450° and larger.

Comparison across conditions:
systematic and random errors

The absolute error plotted in Fig. 5A is a compound measure reflecting both the consistency of the Ss' estimates (that is, by how much an individual's responses to single stimuli deviated from his mean performance, "random error") as well as their calibration (that is, by how much their mean performance deviated from veracity, "systematic error"). Figure 5B and C attempt to separate these factors, using the linear regressions listed in Table 3. The systematic error was calculated in terms of the non-signed difference between these linear fits and veracity (see formula in Fig. 5C for an exact definition), whereas the random error was equated to the (again, non-signed) scatter of single estimates about the corresponding linear fits (see formula in Fig. 5B). The means (across Ss and velocities) of both errors reveal the same differentiation between the passive and active modes, as does the mean absolute error plotted in Fig. 5A, that is, they both were smaller when active, instead of passive, displacements were estimated. This is true at least if displacements exceeding 180° are considered, for which the "active" errors often are only half as large as the "passive" ones. To assess the statistical significance of these differences, we calculated, for each subject and condition, the total RMS value of both types of errors across the whole range of stimulus values considered here (≤450°) and compared the active with the passive conditions by means of Wilcoxon tests for matched pairs. These tests indicated that the RMS-values of both the random- and the systematic-error components were indeed significantly ($P<0.025$) reduced with active rotation; this was true for both modes of estimation (verbal or targeting). The same obviously was true for the mean absolute error, which, as a function of stimulus magnitude, increased at a rate of 33% (PE) and 31% (PT) during passive rotations, but only at rates of 14% (AE) and 11% (AT) during active turning (analysis limited to range ≤450°).

Targeting, as opposed to verbal estimation, had little effect upon the various types of errors. Although a majority of all three types of mean errors plotted in Fig. 5 was slightly smaller when displacement was estimated by targeting instead of verbally, this is not a significant difference.

Finally, we note that, in the two active conditions, the individual "gain" values (slopes of linear regressions, see Table 3), which, together with the intercept values of the linear regression, determine the systematic error, exhibited a clear positive correlation (coefficient of correlation, $r=0.91$). Thus, a subject who overestimated his/her displacement in condition AE was also likely to do so during targeting in condition AT, falling short of the desired displacement.

Discussion

The present work addresses two questions: (1) does the quality of angular displacement perception improve when turning is *active* instead of *passive*, i.e., when there is a convergence of efferent, proprioceptive, and vestibular information instead of only vestibular signals; and (2) does a *targeting* task in any way influence the way angular displacements are perceived? Summarising the above results, a brief answer is: yes, (1) angular orientation during active turning is more precise, and (2) the intention to achieve a specific displacement modifies the perception of *passive* rotation, but not that of *active* turning. However, before we consider these answers in more detail, we shall first discuss some unexpected aspects of the responses recorded with pure vestibular stimulation.

Estimation of passive displacements

It is commonly assumed that the time constant (τ) of vestibular sensation is not longer than 16 s (e.g., Guedry 1974; Young 1981). Given this value, the displacement estimations in our experiments should markedly depend on stimulus velocity. For example, with the "slow", "medium", and "fast" velocities, angular displacements of 450° had durations of 25, 13, and 9 s, respectively; with a time constant of 16 s, the corresponding estimates should differ by as much as 30%. Clearly, however, the results depicted in Fig. 4PE and PT show no signs of a differentiation according to velocity. When it was realized, in the course of the experiments, that velocity apparently does not matter (notwithstanding a few Ss in whom perceived displacement was either positively or negatively correlated with velocity), we began to solicit from our Ss a retrospective description of the time course of their turning sensations during passive rotations. Surprisingly, a majority could not recall having experienced a reduction of velocity in the course a given trial. How can this observation be reconciled with the well-known fact that the sensation of self-turning "normally" declines during constant-velocity rotations?

First, it is interesting to note that Mittelstaedt and Mittelstaedt (1996) in an experiment very similar to ours, except that Ss were standing at various radial distances from the axis of rotation, observed time constants ranging from 22 to 45 s when their Ss stood at the center (as in our experiments). If our Ss had similarly long time constants, velocity would have a much smaller impact than anticipated. For example, given an average τ of 25 s (a conservative value in view of the Mittelstaedts' results), the expected difference between the estimations of 450°-displacements with "fast" or "slow" rotations would reduce to about 16% and be still smaller for smaller displacements. Conceivably, owing to the large variability of the displacement estimations in condition PE, these differences might be too small to be detected.

Second, the time constant of self-turning perception is commonly thought to result from central mechanisms acting to increase the peripheral value of τ. These mechanisms are likely to be context sensitive, a notion that is well illustrated by further results of the Mittelstaedts (*ibid.*): when their Ss were in eccentric positions during rotation, τ increased in proportion to eccentricity, suggesting that the presence of centrifugal forces refreshes the fading vestibular information. On the other hand, upon stopping, the same Ss exhibited time constants of 5–22 s, values which are roughly compatible with the "conventional" 16 s and, noticeably, smaller than the per-rotatory τ of 22–45 s observed when Ss were centered on the axis of rotation. Hence, factors other than centrifugal forces probably also contribute to reducing the per-rotatory decay of vestibular sensation. For example, owing to their upright posture, Ss underwent body sways engendering Coriolis forces, which may have been sensed and used as cues. However, the striking observation here is that, even with "slow" rotations (18.5°/s), an apparent time constant of ≥25 s was obtained. Because with 18.5°/s and normal body-sway amplitudes, the Coriolis forces experienced by our Ss must have been quite small, still other factors must have contributed to enhancing perception.

We hypothesize that our Ss, and possibly also those of the Mittelstaedts' study, had an internal, not necessarily conscious, concept of the events during a stimulus. Specifically, as long as they did not sense an acceleration in the opposite direction, indicative of a clear stop, they apparently assumed that the rotation was going on and merely extrapolated the initial rate of perceived displacement accumulation. Guedry's (1974) observation that some Ss tend to signal 90°-increments at "an apparently autogenous rate" may reflect a similar phenomenon.

Does active turning improve the quality of displacement perception?

The answer to this question is clearly yes, if "quality" is measured in terms of the absolute (non-signed) error, which is reduced by up to 50% during active circling, regardless of whether the perception is probed by verbal estimation or by targeting (cf. Fig. 5A). The improvement was also reflected by the random error (consistency of responses), which was reduced in both active conditions with respect of the corresponding passive ones. Finally, an improvement was also seen when the systematic error, or the veracity of the median estimation curves, was taken as a criterion. In both active conditions, the systematic errors were smaller (Fig. 5C) and the median estimation curves (bold curves in Fig. 4) closer to veracity than in the corresponding passive conditions.

Interestingly, these improvements did not appear to be perceptually registered. For example, although the consistency of verbal estimates was better with active turning, most Ss thought the active task to be more difficult, with a connotation of being less confident of their performance. Whether the failure to correctly appreciate the relative magnitude of their errors owes to the additional

and novel task of achieving a prescribed velocity during active turning or whether it indicates that Ss lack an internal model of their sensory capabilities is an open question as yet.

Clear effects of active, as opposed to passive, turning upon the sensation of self-rotation and upon nystagmus have been noted by Bles and Kapteyn (1977), Correia et al. (1977), Guedry et al. (1978), Bles et al (1983), and others. Typically, with active rotation, these authors observed augmented and prolonged per-rotatory nystagmus and, after rotation, reduced post-rotatory nystagmus, less frequent illusions of counterrotation, and sometimes a sensation of continuing rotation. Except for the latter "antisomatogyral illusion", these effects can also be viewed as improvements, making nystagmus a better reflection of physical truth and abolishing the unwarranted sensation of counterrotation. The "antisomatogyral illusion", on the other hand, is a cost which may be incurred only with prolonged active turning; none of our Ss experienced such an illusion, possibly because they executed only 2 1/4 turns or less, whereas the above authors had their Ss rotate by 4 turns or more; note, however, that Howard et al. (1998) still observed an illusory counterrotation even after their Ss had executed 36 full turns.

Which factors are responsible for the improved quality of the sensation of self-rotation observed during active turning? Straightforward explanations that readily come to mind, such as step counting or time estimation, do not apply. None of the Ss reported step counting during the interview following the experiments. Moreover, we had also deliberately avoided any instruction that could have directed Ss' attention at their steps and, therefore, had not asked them to observe a certain pace of stepping. Time estimation had been made difficult, if not impossible, by randomly varying between three velocity levels. Moreover, time could as well have been used during passive rotation and, therefore, cannot explain the difference between active and passive conditions.

Although the velocity profile during active circling was, on a global scale, similar to that used in passive rotation, it differed from the passive profile by being modulated at the pace of stepping. From the point of view of the peripheral vestibular system, which appears to be a fairly linear one, this modulation would not change the result of a path integration aimed at obtaining a measure of angular displacement. However, at more central stages of the vestibular pathway to conscious perception, the modulation could prime the hypothesized extrapolation of the initial rate of growth of perceived displacement, so as to reduce its variability in comparison to passive rotation.

Yet, there can be little doubt that the major cause for the improvements observed during active turning comes from the proprioceptive and efferent signals generated during these movements. Mittelstaedt and Glasauer (1991) have coined the term "*substratal idiothesis*" to designate all efferent and proprioceptive information related to an individual's motion relative to a substrate (e.g., our platform), as opposed to *inertial idiothesis*, which refers to vestibular mechanisms of movement detection. Conceivably, besides corollary discharges of ongoing motor activity, the efferent contribution may also reflect the Ss' plans and intentions. These may not only aim at achieving a desired displacement relative to a substrate, but also at controlling displacement in space by having the active movement generate a certain pattern of vestibular stimulation. Therefore, a distinction between *efferent idiothetic* and *substratal idiothetic* signals would seem to be appropriate. Yet, in most active motions, these two types of information will be inseparable; for short, we are referring to their compound content as "*efferentsensory*" information.

Pure efferentsensory stimulation, which arises during circular walking on a tread-mill with no effective displacement in space, is known to easily evoke an illusory sensation of self-rotation in space (Bles and Kapteyn 1977; Bles 1981; Bles et al. 1984). Similarly, Lackner and DiZio (1984) observed an illusory self-motion in stationary, seated Ss who stepwise propelled a movable disk with their feet. Hlavacka et al. (1992) and Mergner et al. (1993) have shown that low-frequency proprioceptive stimulation of the leg joints, with little or no efferent contribution (trunk stationary, leg passively rotating in contact with a moving substrate), is also capable of evoking illusory self-rotation. Even rotations of the arm in touch with a moving drum can elicit this sensation (arthrokinetic circularvection; Brandt et al. 1977). Taken together, these observations strongly support the intuitive notion that efferent and substratal idiothesis contribute to the perception of self-turning in active tasks.

The question remains, however, whether it is the combination of vestibular *and* efferentsensory information which reduces the estimation errors during active turning, or whether the efferentsensory information merely supersedes the vestibular one, causing the observed improvement all by itself. For example, the mean RMS value of the random error calculated for condition AE was smaller than that obtained for PE by a factor of roughly $\sqrt{2}$. One possible interpretation of this result is that the random errors of the efferentsensory channel have a similar magnitude as those of the vestibular channel, and that the two channels are averaged during active turning. An alternative interpretation holds that the efferentsensory channel is more accurate (error by a factor of $\sqrt{2}$ smaller) than the vestibular one, which, therefore, would be discarded during active turning. These questions require a more detailed characterization of the efferentsensory channel than is available hitherto. Bles (1981; his Fig. 3.2) found displacement perception during pure efferentsensory stimulation to be as veridical and consistent as during combined vestibular *and* efferentsensory stimulation, an observation that would support the second interpretation; clearly however, Bles' single datum (one velocity, one amplitude) is insufficient for any firm conclusion. On the other hand, experiments by Glasauer et al. (1994) in labyrinthine-defective patients (though during linear locomotion) suggest that, without vestibular contribution (from the otolith system in their case),

targeting accuracy of active motion deteriorates, implying that full perceptual accuracy requires the presence of both inertial *and* efferentsensory information.

How does sensory fusion work?

The above question touches upon a basic problem of sensory convergence, that is, by which rules are the various afferents combined to yield a fused, unified representation of a behavioral situation? For the case of visual-vestibular convergence, Robinson (1977) suggests a straightforward summation, at the level of the vestibular nuclei, of the vestibular high-pass signal [transfer function $H(\omega)$; ω, angular frequency] with a complementary visual low-pass signal $L(\omega)$, such that $L(\omega)+H(\omega) \approx g_0 =$ constant, the result being a frequency-weighted average. An explicit model of self-rotation perception based on the notion of complementary visual and vestibular signals has been put forward by Mergner et al. (1995). Matters become complicated, however, if this type of convergence is extended to more inputs, in particular inputs which are "switched" on and off, depending on the behavioral situation. For example, arthrokinetic signals are held to be remotely similar to the visual input in that they also have low-pass properties (Bles 1981). A summation of an arthrokinetic low-pass signal with the vestibular high-pass has been invoked to explain the absence of illusory counterrotations after voluntary circular stepping (Bles et al. 1984) as well as the longer persistence of per-rotatory nystagmus and the absence of post-rotatory nystagmus in seated Ss propelling and stopping themselves by pedaling their hand or feet on a stationary surface (Guedry and Benson 1983). However, what happens if arthrokinetic stimulation is added to visual-vestibular stimulation in a lighted environment? Obviously, given $L(\omega)+H(\omega) \approx g_0$, the total gain now would equal $g_0 + L_a(\omega)$, with $L_a(\omega)$, the contribution of the proprioceptive (arthrokinetic) signals, varying according to whether only the feet or only the arms, or both, are passively or actively involved in the rotation. Obviously, if perceived magnitude of self-rotation were based on such a straightforward addition of afferents, it would vary accordingly. However, as pointed out by Bles (1981), the magnitude of perceived self-rotation does not depend on whether it is induced by sensory systems individually or by their congruent combination. This is also what the present experiments indicate: although it engaged an additional sensory channel, active circling did not increase displacement perception in comparison to passive rotation, but actually decreased its magnitude slightly (cf. Fig. 4). Clearly, if summation is to be the basic mechanism of sensory convergence for the perception of self-rotation, it must be complemented by a normalization procedure to make it independent of the number of contributing signals; that is, the signals must be averaged. Averaging of vestibular and proprioceptive inputs has indeed been suggested as a mechanism of sensory fusion (Howard et al. 1998), albeit only with reference to

the generation of per- and post-rotatory nystagmus. It is difficult to imagine the details of a such normalization mechanism, which would require a book-keeping of which sensory channels ore "on" and which "off" at any moment. Therefore, the mechanism of sensory fusion, at least the one underlying the perception of active self-turning, is likely to be non-linear. In this laboratory, we are currently pursuing the idea that the fusion takes place on neural maps with excitatory and inhibitory lateral connections of the type suggested by Amari (1977), which would code magnitude by the center of gravity of an activity distribution.

Where are the arthrokinetic and other proprioceptive signals related to active circling being merged with vestibular and visual afferents? One candidate structure is certainly the vestibular nuclei, which are known to receive somatosensory information in addition to their vestibular and visual inputs. Although a large percentage of this input is devoted to neck afferents, vestibular neurons can also be activated by limb movements (Frederickson et al. 1965; Rubin et al. 1977). Likewise, in the vestibular thalamus, a large proportion of neurons respond to limb movements (Büttner and Henn 1976; Deecke et al. 1977). Finally, at the level of the vestibular cortical areas, deep somatic afferents, mostly from joint receptors, are known to project to area 2v (Frederickson et al. 1974), whereas area 3a is characterized by a convergence of vestibular signals and muscle-spindle afferents (Ödkvist et al. 1974). More recently, a convergence of vestibular, proprioceptive, and optokinetic inputs also has been demonstrated in the parieto-insular cortex (Grüsser et al. 1990). The parieto-insular cortex and area 3a are bilaterally connected, forming an "inner cortical vestibular circuit" that receives signals from the primary somatosensory cortex (Guldin et al. 1992). Of these structures, the parieto-insular cortex, which is considered to be a vestibular core region (Guldin and Grüsser 1998), would be well suited for the ultimate assembly of a unified representation of head and trunk behavior in space. It is unlikely, however, that the merging of the many sensory modalities contributing to self-motion perception is restricted to any single area or any single hierarchical level. Rather, the cortical vestibular areas would seem to expand on a multisensory integration that already takes place in the brain stem and the thalamus, but which, in its low-level version, does not yet well abstract the Gestalt and magnitude of self-rotation from the variations and particularities of the contributing cues.

Modification of displacement perception by behavioral context: the effect of "targeting"

Various types of "targeting" have been considered during research into navigation and path integration. In experiments on *linear* displacement, a visual landmark is frequently shown to Ss, who then have to walk blindfolded to this target (e.g., Glasauer et al. 1994) or have to signal when they pass by the target while being pas-

sively moved (e.g., Israël et al. 1993). Others have asked their Ss to reproduce a previously experienced passive displacement by a self-controlled ride on a vehicle (e.g. Israël et al. 1997). In investigations dealing with *angular* displacements, Ss have been rotated away from a home position and, then, had to return to this position by controlling the movement of a turning chair (e.g., Metcalfe and Gresty 1992; Israël et al. 1996) or have been asked to drive their chair to a verbally specified position (Israël et al. 1995). None of these investigations had in mind to learn whether displacement estimation is independent of its behavioral context or not, whereas we introduced targeting as an additional condition, for just this reason, using a procedure very similar to that of Israël et al. (1995). Note, however, that, whereas these authors specified angular *positions*, we had our Ss match their passive or active self-rotation to previously specified angular *displacements*, because the notion of position becomes equivocal when rotations exceed more than one full turn.

We had hypothesized that the task of targeting (achieving a prescribed displacement) would improve the veracity and reliability of displacement perception because, here, it becomes a behaviorally relevant information. This hypothesis was not born out. Neither veracity nor consistency (random error) was significantly improved by targeting. Yet, one significant difference between verbal estimation and targeting did occur, although only in the passive mode: with *verbal* estimation, the median estimation curve was characterized by an overestimation of small displacements, which progressively turned into an underestimation of large ones ("saturation"). In contrast, with *targeting*, only small displacements were (slightly) underestimated, whereas a conspicuous overestimation (= undershoot of the targeting movement) occurred when medium and large displacements were required, with no signs of saturation. This is surprising, even if one takes into account the possibility that the perceptual time constant might be significantly longer than 16 s. From the saturation of displacement perception observed with condition PE, one would expect that Ss disproportionately prolong their rotation in condition PT when trying to match their perception to increasingly larger prescribed displacement magnitudes. We are aware of no obvious methodological reasons that could be held responsible for the large undershoot. Also, others have observed overestimations (=undershoots of targeting) in comparable situations, albeit with stimuli of shorter duration: the Ss of Israël et al. (1995) undershot targets of 360° by 13% (a 15% overestimation of self-displacement). Results from the same group obtained in Ss who had to drive themselves back to their initial position after being rotated by 180° indicate overestimations of up to 20% (Israël et al. 1996). Significantly, both investigations also concur with ours in that things are reversed at the low end of the stimulus range, because small displacements were *under*estimated (i.e., movements aimed at targets close to the start position were too large).

The reversal from over- to undershoot is reminiscent of the "range effect", a contraction bias observed with rapid goal-directed movements of the extremities and of the eyes (Poulton 1981), which causes the smallest target distances occurring in an experiment to be overshot, whereas the large distances are undershot. However, whereas the range effect described by Poulton concerns ballistic movements that cannot be corrected in flight, our Ss could continuously monitor the perceptually signaled growth of their displacement and check it against the desired value. Moreover, although we had asked our Ss to try and use a single rotation to reach the desired displacement, they also had been instructed to correct their position if they felt they had not achieved it. Yet, corrective movements were rare (5%). Finally, if a range effect is invoked to "explain" the difference between verbal estimation and targeting during passive rotation, one should expect a similar difference to occur during active turning. However, the difference between the median estimation curves obtained with verbal estimation (AE) and targeting (AT) was not significant and too small to warrant such a claim. It is interesting to note, in this context, that during active turning there was not only little difference between targeting and verbal estimation with regard to the population medians, but that also the Ss' idiosyncratic variations were correlated: Ss who overestimated their displacement upon verbal rendition also did so during targeting, suggesting that both conditions (AE and AT) sampled perceptions based on the same internal calibration. No such correlation could be detected between the passive conditions PE and PT; it is unclear whether this lack of individual correlation is a further sign of the difference between the two passive modes or whether it merely results from the large random errors occurring during passive rotation.

Finally, a caveat must be issued regarding the differential effects of targeting in the passive and active modes: the way the rotations were generated in AE and AT was identical, whereas PT differed from PE in that the Ss, instead of computer software, controlled the platform drive. Therefore, we cannot completely rule out that a better agreement between the two passive conditions would have resulted if Ss had been given the task of merely stopping an otherwise software-controlled rotation.

References

Amari S (1977) Dynamics of pattern formation in lateral-inhibition type neural fields. Biol Cybern 27:77–78

Barr CC, Schultheis LW, Robinson DA (1976) Voluntary, nonvisual control of the human vestibulo-ocular reflex. Acta Otolaryngol (Stockh) 81:365–375

Bles W (1981) Stepping around: circular vection and Coriolis effects. In: Long J, Baddeley A (eds) Attention and performance IX. Lawrence Erlbaum, Mahwah, pp 47–61

504

Bles W, Kapteyn TS (1977) Circular vection and human posture. I. Does the proprioceptive system play a role? Agressologie 18:325–328

Bles W, Klören T, Büchele W, Brandt T (1983) Somatosensory nystagmus: physiological and clinical aspects. Adv Otorhinolaryngol 39:30–33

Bles W, Jong JMBV de, Wit G de (1984) Somatosensory compensation for loss of labyrinthine function. Acta Otolaryngol (Stockh) 97:213–221

Borenstein J, Everett HR, Feng L (1996) Where am I? Sensors and methods for autonomous mobile robot positioning. University of Michigan. Downloadable from http://www-personal.engin.umich.edu/~johannb/position.htm

Brandt T, Büchele W, Arnold F (1977) Arthrokinetic nystagmus and ego-motion sensation. Exp Brain Res 30:331–338

Büttner U, Henn V (1976) Thalamic unit activity in the alert monkey during natural vestibular stimulation. Brain Res 103:127–132

Correia MJ, Nelson B, Guedry FE (1977) Antisomatogyral illusion. Aviat Space Environ Med 48:859–862

Deecke L, Schwarz DWF, Fredrickson JM (1977) Vestibular responses in the rhesus monkey ventroposterior thalamus. II. Vestibulo-proprioceptive convergence at thalamic neurons. Exp Brain Res 30:219–232

Elliot D (1987) The influence of walking speed and prior practice on locomotor distance estimation. J Mot Behav 19:476–485

Frederickson JM, Schwarz DWF, Kornhuber HH (1965) Convergence and interaction of vestibular and deep somatic afferents upon neurons in the vestibular nuclei of cat. Acta Otolaryngo (Stockh) 61:168–188

Frederickson JM, Kornhuber HH, Schwarz DWF (1974) Cortical projections of the vestibular nerve. In: Kornhuber HH (ed) Handbook of sensory physiology, vol VI/2. Vestibular system. Springer, Berlin Heidelberg New York, pp 565–582

Glasauer S, Amorim MA, Vitte E, Berthoz A (1994) Goal-directed linear locomotion in normal and labyrinthine-defective subjects. Exp Brain Res 95:323–335

Grüsser O-J, Pause M, Schreiter U (1990) Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys. J Physiol 430:537–557

Guedry FE (1974) Psychophysics of vestibular sensation. In: Kornhuber HH (ed) Handbook of sensory physiology, vol VI/2, Vestibular system. Springer, Berlin Heidelberg New York, pp 1–154

Guedry FE, Benson AJ (1983) Modification of per- and postrotatory responses by voluntary motor activity of the limbs. Exp Brain Res 52:190–198

Guedry FE, Mortensen CE, Nelson JB, Correia MJ (1978) A comparison of nystagmus and turning sensations generated by active and passive turning. In: Hood JD (ed) Vestibular mechanisms in health and disease. Academic Press, London, pp 317–325

Guldin WO, Grüsser O-J (1998) Is there a vestibular cortex? Trends Neurosci 21:254–259

Guldin WO, Akbarian S, Grüsser O-J (1992) Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: a study in squirrel monkeys (*Saimiri sciureus*). J Comp Neurol 326:375–401

Hlavacka F, Mergner T, Schweigart G (1992) Interaction of vestibular and proprioceptive inputs for human self-motion perception. Neurosci Lett 138:161–164

Howard IP, Zacher JE, Allison RS (1998) Post-rotatory nystagmus and turning sensations after active and passive turning. J Vestib Res 8:299–312

Israël I, Chapuis N, Glasauer S, Charade O, Berthoz A (1993) Estimation of passive horizontal linear whole-body displacement in humans. J Neurophysiol 70:1270–1272

Israël I, Sievering D, Koenig E (1995) Self-rotation estimate about the vertical axis. Acta Otolaryngol (Stockh) 115:3–8

Israël I, Bronstein AM, Kanayama R, Faldon M, Gresty MA (1996) Visual and vestibular factors influencing vestibular "navigation". Exp Brain Res 112:411–419

Israël I, Grasso R, Georges-Francois P, Tsuzuku T, Berthoz A (1997) Spatial memory and path integration studied by self-driven passive linear displacement. I. Basic properties. J Neurophysiol 77:3180–3192

Lackner JR, DiZio P (1984) Some efferent and somatosensory influences on body orientation and oculomotor control. In: Spillmann L, Wouten BR (eds) Sensory experience, adapatation, and perception. Lawrence Erlbaum, Mahwah, pp 281–301

Lackner JR, DiZio P (1988) Visual stimulation affects the perception of voluntary leg movements during walking. Perception 17:71–80

Laurent M, Thomson JA (1988) The role of visual information in control of a constrained locomotor task. J Mot Behav 20:17–37

Mergner T, Hlavacka F, Schweigart G (1993) Interaction of vestibular and proprioceptive inputs. J Vestib Res 3:41–57

Mergner T, Schweigart G, Kolev O, Hlavacka F, Becker W (1995) Visual-vestibular interaction for human ego-motion perception. In: Mergner T, Hlavacka F (eds) Multisensory control of posture. Plenum Press, New York, pp 157–167

Metcalfe T, Gresty MA (1992) Self-controlled reorienting movements in response to rotational displacements of normal subjects and patients with labyrinthine disease. Ann NY Acad Sci 656:695–698

Mittelstaedt M-L, Glasauer S (1991) Idiothetic navigation in gerbils and humans. Zool Jb Physiol 95:427–435

Mittelstaedt M-L, Mittelstaedt H (1996) The influence of otoliths and somatic graviceptors on angular velocity estimation. J Vestib Res 6:355–366

Ödkvist LM, Schwarz DWF, Fredrickson JM, Hassler R (1974) Projection of the vestibular nerve to the area 3a arm field in the squirrel monkey. Exp Brain Res 21:97–105

Poulton EC (1981) Human manual control. In: Brooks VB (ed) Handbook of physiology, section I. Neurophysiology, vol II. Motor Control. American Physiological Society, Bethesda, pp 1337–1389

Rieser JJ, Asmead DH, Talor CR, Youngquist GA (1990) Visual perception and the guidance of locomotion without vision to previously seen targets. Perception 19:675–689

Robinson DA (1977) Linear addition of optokinetic and vestibular signals in the vestibular nucleus. Exp Brain Res 30:447–450

Rubin AM, Liedgren SR, Miline AC, Young JA, Fredrickson JM (1977) Vestibular and somatosensory interaction in the cat vestibular nuclei. Pflügers Arch 19:155–160

Young LR (1981) Perception of the body in space: mechanisms. In: Geiger SR (ed) Handbook of physiology, section 1. The nervous system, vol III. American Physiological Society, Bethesda, pp 1023–1066