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Fusion of vestibular and podokinesthetic information during self-turning towards instructed targets

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Abstract When observers step about their vertical axis (“active turning”) without vision they dispose of essentially two sources of information that can tell them by how much they have turned: the vestibular cue which reflects head rotation in space and the “podokinesthetic” cue, a compound of leg proprioceptive afferents and efference copy signals which reflects the observer’s motion relative to his support. We ask how these two cues are fused in the process leading to the perception of self-displacement during active turning. To this end we compared the performance of observers in three angular navigation tasks which differed with regard to the number and type of available motion cues: (1) Passive rotation, vestibular cue (*ves*) only; observers are standing on a platform which is being rotated. (2) Treadmill stepping, podokinesthetic cue (*pod*) only; observers step counter to the rotating platform so as to remain stable in space. (3) Active turning, *ves* and *pod* available; observers step around on the stationary platform. In all three tasks, angular velocity varied from trial to trial (15, 30, 60°/s) but was constant during trials. Perception was probed by having the observers signal when they thought to have reached a previously instructed angular displacement, either in space or relative to the platform (“target”; range 60–1080°). Performance was quantified in terms of the targeting gain (displacement reached by the observer divided by target angle) and of the random error (E_r), which records an observer’s deviation during single trials from his average performance. Confirming previous observations, E_r was found to be significantly smaller during active turning than during passive turning, and we now complement these observations by showing that it is also significantly smaller than during treadmill stepping. This behaviour of E_r is compatible with the idea that *ves* and *pod* be averaged during active turning. On the other hand, the observed characteristics of the targeting gain (G_T) support this idea only for the case of fast

rotations (60°/s); at lower velocities, the gain found during active turning was clearly not the average of the G_T values recorded in the passive and the treadmill modes. We therefore also discuss alternative scenarios as to how *ves* and *pod* could interact, among these one based on the concept of a vestibular *eigenmodel*. A common denominator of these scenarios is that *ves* assumes the role of a prerequisite for an optimal use of *pod* during turning on a stationary support, without itself entering the calculation of displacement perception; this perception would be based exclusively on *pod*. Finally, it was a consistent observation that during passive rotations cognitive mechanisms fill in for the decaying vestibular signal in the context of the present navigation task, enabling observers to achieve large displacements surprisingly well although the duration of these movements exceeds by far the conventionally cited value of the central vestibular time constant (=20 s).

Keywords Sensory fusion · Vestibular-proprioceptive convergence · Vestibular system · Podokinesthetic system · Treadmill stepping · Active turning · Passive turning · Navigation · Perception of angular displacement

Introduction

It is generally assumed that the robustness of sensory perception in everyday life is due, at least partially, to “sensory fusion”, i.e. the ability to improve the quality of sensation by combining different sources of information about the same sensory event. The perception of angular self rotation offers particularly illustrative examples of this principle. Although visual landmarks play a dominant role for our orientation when we rotate in a lighted environment, we fortunately also dispose of optokinetic (optic flow), vestibular, proprioceptive and efference copy signals which co-determine our perception and which take over when landmarks cannot help (when unavailable or during events that are too fast to be visually

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tracked). It is well known that even in darkness, when also the optokinetic contribution is inoperative, we still are able to perceive displacements of the self (for a review see Guedry 1974). During active turning in darkness, orientation primarily is supported by two sensory mechanisms: (1) “*inertial idiothesis*” and (2) “*substratal idiothesis*” (Mittelstaedt and Glasauer 1991); the former is provided by vestibular afferents signalling body angular velocity in space (on the condition that there is no head-to-body rotation) while the latter rests on proprioceptive afferents from hip, legs and feet signalling our rate of stepping and the amount of angular rotation per step relative to our support. A third, conceivably important, contribution may arise from signals reflecting the efference sent to the leg motor system (*efference copy*) which also contain information about our stepping on the support.

Little is known, so far, as to how the various sensory messages are fused to yield a unitary percept of the self's situation in space. Drawing on notions originating from linear systems theory, Howard (1997) advanced the hypothesis that fusion might be based on a weighted averaging of sensory signals s_i , with the fused signal equaling $s = \sum w_i s_i / \sum w_i$ and weights w_i chosen to be reciprocals of the signal variances. Such a scheme would minimise the variability of the resulting perception which would become smaller than the variability of any perception based on only one of the involved sensory modalities; for example, fusing two sensory signals of equal variance would reduce variance by a factor of $\sqrt{2}$. The predictions of this linear hypothesis can be tested if one succeeds to isolate the sensory sources contributing to the fused perception. For example, one can compare the perceptions evoked by passive rotations, which only stimulate the vestibular sensor, to those arising from active rotations during which also the somatosensory and efference copy mechanisms are being active. This approach has been used by Bles (1981) who recorded the mean perceived velocity during passive rotations and during circular walking, and by Bakker et al. (1999) who had subjects (Ss) either steer the rotation of a turning chair in complete darkness (by controlling motor current) or step about their vertical axis so as to achieve an instructed angular displacement. The latter authors report a clear reduction in constant error (mean signed deviation from veracity) and a small reduction in variable error (intrasubject SD) upon active turning (vestibular, somatosensory and efference copy sensations combined) as compared to passive rotation (vestibular only stimulation). Similar observations have been made in this laboratory using both the method of Bakker et al. and retrospective displacement estimations after passive rotation or active circular stepping (Jürgens et al. 1999). Finally, also Marlinsky (1999) who compared passive and active rotations in sitting Ss (active rotation achieved by stepping on the floor) reports a slight (albeit not significant) reduction in variable error in the active condition.

Although these results are compatible with the notion of a fusion of vestibular and leg proprioceptive afferents

by way of weighted averaging in as much as the variable error was reduced during active turning, they nonetheless remain inconclusive because in all studies only one of the sensory sources contributing to self-turning perception (the vestibular one) had been isolated. It could as well be that *no* fusion takes place during active turning. Instead, the somatosensory and efference copy inputs simply might supersede the vestibular afferents if turning is not passive, with the smaller errors observed during active turning reflecting inherently superior characteristics of these latter two signals in comparison to the vestibular ones. Clearly, for a definite proof of the weighted average hypothesis one would have to show: (1) that the variable error associated with the proprioceptive and efferent sources of information, like that arising during vestibular perception, is larger than the error observed during active turning when all sources are activated and (2) that the constant error is indeed the *average* of the errors inherent to each of the monomodal perceptions.

In the intact human it is experimentally difficult to separate the somatosensory and efference copy contributions from each other and so, for the sake of brevity, we shall call their combined information *podokinesthetic*, a slight modification of the term “podokinetic” coined by Weber et al. (1998) to designate the “somatosensory-motor system controlling locomotor trajectory through foot contact with the floor”¹. While the specific contributions of the efference copy and of the somatosensory afferents cannot be singled out, their compound – the podokines-*thetic* information – can be examined in isolation using a treadmill paradigm where Ss are at the centre of a rotating platform and step counter the platform rotation so as to remain stationary in space (mean vestibular input approximately 0). In the past, rotatory treadmill stepping has been used to investigate the induction of circularvection by proprioceptive stimulation (“apparent stepping around”; Bles and Kapteyn 1977), the modulation of perceived step stride magnitude by optokinetic stimulation (Lackner and DiZio 1988), postrotatory nystagmus and after-sensations following apparent stepping around (Howard et al. 1998) and perceptual after-effects of long-term unidirectional stepping (“podokinetic after-rotation”; Weber et al. 1998).

There appears to be only one study (Bles 1981) in which a quantification of the perceptions arising during treadmill stepping has been attempted. In this study, Bles had Ss indicate perceived 360° turnings of the self during various monomodal and combined vestibular, visual and somatosensory stimulations, including a pure somatosensory (i.e. treadmill) condition which elicited apparent stepping around. Except for pure vestibular stimulation which differed from all other conditions, Bles obtained no differences in perceived 360° rotations among his various stimulus conditions, including active circling and treadmill stepping. This observation would seem to contradict the weighted averaging hypothesis; the vestib-

¹ We previously have used the term “efferentsensory” (Jürgens et al. 1999) which was meant to underline the notion of an efferent contribution

ular signal being different, the fused signal cannot equal the podokinesthetic one and, at the same time, be a vestibulo-podokinesthetic average.

However, we felt that Bles' data, which represent mean values across 18 continuous revolutions at a single velocity (vestibular stimulation: 2 revolutions), are still insufficient for more definite conclusions. We therefore wished to expand on our previous work (Jürgens et al. 1999) by measuring and comparing the vestibular and podokinesthetic contributions to perception of self-turning, and their interaction during active circling, in a more systematic way. To probe these contributions, several methods are available. Subjects could: (1) deliver concurrent or retrospective estimations of perceived turning velocity, (2) indicate perceived angular displacement either upon request or retrospectively, or (3) indicate when, according to their perception, they have reached a previously instructed angular displacement. From a behavioural point of view, indicating or achieving an angular displacement bears more resemblance to the natural task of navigation than the estimation of angular velocity or perceived turning intensity (which has been extensively studied by classic vestibular psychophysics; see reviews by Guedry 1974; Dichgans and Brandt 1978). Indeed, what matters for the orientation in space is not so much turning velocity but its consequence, angular displacement. Because, to our experience, verbal indications of achieved displacement are associated with both large *intraindividual* and large *interindividual* scatter as well as being affected by anchor effects, we chose the third of the above methods, requiring Ss to indicate when an instructed displacement has been reached ("targeting"). In more recent studies, the method of targeting has been repeatedly used to gauge passive and active locomotor perception during both linear motion (see, for example, Rieser et al. 1990; Glasauer et al. 1994; Mittelstaedt and Mittelstaedt 2001), and circular motion [beside the aforementioned studies of Bakker et al. (1999), Jürgens et al. (1999) and Marlinsky (1999), one can also cite here the examples of Metcalfe and Gresty (1992) and Israël et al. (1995, 1996) who used targeting in the sense of reproducing previously experienced passive rotations].

The task of targeting is readily conveyed to Ss undergoing passive and active self-rotation. However, with treadmill stepping it requires some metaphorical effort. Treadmill stepping does not always evoke the illusion of apparent stepping around, i.e. of a circling of the self in space. Whereas the Ss of Bles (1981) apparently all entered a regime of podokinesthetic circularvection after some variable initial delay, a reliable occurrence of apparent stepping around within two or three revolutions of the platform (the range of displacements considered in the present study) is not the rule, to our experience. Therefore, during treadmill stepping, we had to replace the indication of self-turning in space by judgements of the amount of relative displacement between the self and the platform or of platform rotation in space. This substitution may raise the concern whether at all the thus-

obtained quantitative measures allow inferences regarding the podokinesthetic contribution to the perception of self-rotation during stepping on *firm* ground. We shall address this point in the Discussion.

In summary, the present study compares the targeting performance of human Ss during passive rotation, during circular treadmill stepping and during circular stepping on firm ground in an attempt to further characterise the way by which the information of two *different* sensory systems (vestibular and podokinesthetic) concerning the *same* physical event is being integrated.

Materials and methods

Subjects

Twenty-eight paid volunteers (mostly undergraduate students), aged 17–32 years served as Ss. None of them had any known neurological disease. Subjects gave their informed consent after having learned the general goals and procedures of the experiment which had been approved by the local ethics committee. In explaining the experiment, care was taken to keep Ss naive as to the specific goals of the experiment in order to minimise the risk that their responses would be affected by preconceptions. The data to be reported here are based on two series of experiments which were carried out at a year's distance with only slight differences in procedures (cf. below). Sixteen of the Ss (eight male, eight female) participated in the first series, and the remaining 12 (six male, six female) in the second one.

Equipment

The equipment and most of the procedures have been described in an earlier paper (Jürgens et al. 1999). Briefly, Ss were at the centre of a turning platform, standing either motionless (relative to the platform) or turning about their vertical axis by small steps. Platform rotations about the vertical axis could be generated by a servo motor under computer control and were free of perceptible vibrations or jolts. Subjects' 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 by the subject. Integrated into the harness was a wireless headphone delivering a masking noise during rotations and serving verbal communication. Head-to-trunk rotations were minimised by an orthopaedic neck collar.

Experimental conditions and procedures

First series

Subjects were presented with three turning conditions: *passive* (V; pure vestibular stimulation), *treadmill* (P; podokinesthetic stimulation) and *active* (PV; podokinetic and vestibular). Each condition was administered in a separate block of about 35 min duration, in the course of 1 day, with the order of presentation randomised across Ss. The stimuli of each block consisted of rotations at two velocities (30 and 60°/s) in either direction, each associated with ten different "target angles" (details below) ranging from 90 to 720° at 30°/s, and from 150 to 1080° at 60°/s. The resulting 40 stimuli (2 velocities × 2 directions × 10 target angles) occurred in pseudorandom order determined by three different lists which were permuted among Ss and conditions in a balanced way.

Subjects' perceptions were assessed by measuring their *targeting* performance. Before each turning a *desired displacement* (D_d ; also called "target" for short) was announced to Ss, specified in

degrees or number of turns (for example, “270°” or “three-quarters of a turn”). A warning tone (1 kHz) then was sounded and rotation started. During the rotation Ss were to keep track of their angular displacement (relative to space or to the platform; details below) and to press a hand-held signal button when they felt that the desired displacement had been reached. Thereafter the rotation was decelerated to zero, and Ss rated how confident they were about their performance using German school marks (1–6: 1, absolutely sure; 6, absolutely unsure). Between successive stimuli, there was a pause of varying length, depending on the duration of the preceding stimulus (approximately 1.5 times stimulus duration, but never less than 20 s). Before starting a new condition, Ss were given five practising trials with feedback about performance after each trial, whereas no feedback was given during the experiments proper. At the end of the experiment, Ss were asked to compare the subjective difficulty of estimation across the three conditions and to report their personal observations regarding possible after-effects and particular strategies used for estimation.

Details of conditions

Condition V: passive rotation in darkness. Subjects stood motionless on the turning platform and underwent passive whole body rotations consisting of a period of constant velocity ($v_c=30$ or $60^\circ/s$) flanked by smooth acceleration and deceleration periods of duration T , defined by:

$$v(t) = v_c \cdot 0.5 \cdot (1 - \cos(\pi \cdot t/T)); \quad v(t), \text{ velocity at time } t$$

with $T=0.5$ ($v_c=30^\circ/s$) or 1.0 s ($v_c=60^\circ/s$) during acceleration and twice these values for the deceleration after Ss' button press. Subjects were instructed 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. If large displacements were required it was recommended that they accumulate portions of 90° in their mind.

Condition P: treadmill stepping in darkness. The platform was rotated as in condition V. During rotation, Ss were to step about their vertical axis in the opposite direction while holding to an earth-fixed rail so as to stabilise themselves in space; stepping occurred in such way that the axis was between Ss' feet and that the feet moved along a concentric circle of diameter 20–30 cm. To free both hands for grasping the rail, the signal button was mounted on the rail at thumb's reach in this condition. Subjects were instructed to track angular self-displacement *relative* to the platform and to indicate when it had reached the desired target value. Two alternative modes of mental tracking were suggested to them: (1) imagine a degree scale painted on the platform and concentrate on body displacement with respect to this scale or (2) imagine a pointer painted on the platform and track its rotation in space while considering the self as a landmark fixed in space. Subjects were instructed to select their preferred mode during the practising trials.

Condition PV: active turning in darkness. Subjects first were trained to smoothly step about their vertical axis (using the same pattern of foot movement as in P, i.e. to “turn on the spot”), at approximately constant velocity and, in doing so, to choose among the two velocities, 30 and $60^\circ/s$ (step rates and widths at Ss' discretion). Training was generally completed in about 5 min. In the experiment proper, in addition to the desired displacement, the experimenter also announced the desired turning velocity and direction (drawn from the same lists as used to control platform rotation during passive turning and treadmill stepping) before each trial. After the 1-kHz warning tone, Ss then were to step around at the indicated velocity and to press the button upon reaching the desired displacement; only thereafter Ss were allowed to stop their turning.

Second series

A second series of experiments was carried out with a new group of Ss ($n=12$) with the aim of testing the reliability of the phenom-

na observed in the first series and, by the same token, of studying a larger range of turning velocities. In addition it also served as a baseline experiment for a different study with the same Ss. Its conditions (V, P and PV) were similar to those of the first series except for the following changes:

1. There were three velocities (15, 30 and $60^\circ/s$), instead of only two, and eight target angles ranging from 150 to 450° ($15^\circ/s$ rotations), to 720° ($30^\circ/s$), or to 900° ($60^\circ/s$).
2. In conditions P and PV, Ss' stepping was guided by a loose handle suspended from the ceiling which was stationary in P and rotated at the desired speed in PV. Subjects were to gently hold it between their fingers (right hand; signal button in left hand) while keeping their arm in a constant, slightly flexed, position with respect to their trunk.
3. The collection of school marks after each single trial was discontinued and replaced by a global scoring of self-confidence and task difficulty to be delivered in the course of retrospective interviews after completion of each condition (using again a scale ranging from 1 to 6). These interviews also inquired whether Ss had experienced a rotation at *constant* velocity, or whether they had felt an acceleration or a deceleration.
4. Being part of a larger study there was always one condition that was tested on a different day than the other two (determined by a global randomisation scheme).

Data acquisition and analysis

The positions and velocities of the turning platform and of Ss' head relative to space were sampled at 1,000 Hz and stored on disk together with the pushbutton signal, and Ss' confidence ratings were typed in by the experimenter. For analysis, *achieved displacement* (D_a) was determined by measuring the angular displacement of Ss' head accumulated between turning onset and the instant of button press. For each subject, each experimental condition and each of the turning velocities, the linear regression of achieved displacement on desired displacement (D_d) was then calculated to obtain the coefficients D_0 and b of the linear fit of D_a , given by $D_f = D_0 + b \cdot D_d$. Finally the quality of targeting of each single trial was characterised by two measures: (1) the *targeting gain*, $G_T = D_a/D_d$, which indicates how closely achieved displacement matched desired displacement (ideal value: $G_T=1$) and (2) the *random error*, $E_r = |D_a - D_d|$ which provides a measure of within-session variability by noting how much D_a deviated during single trials from a subject's average behaviour characterised by the linear fit D_f (see example in Fig. 1 *upper panel*).

To evaluate the effect of turning mode (V, P or PV), turning velocity and magnitude of desired displacement, three-way repeated measures ANOVAs were conducted using commercial software (Statistica). Of the factor *desired displacement*, only those levels were included which occurred with every velocity (first series, eight levels ranging from 150 to 720° ; second series, five levels ranging from 150 to 450°). Scheffé tests were used for *post hoc* comparisons. Effects will be considered significant if $P < 0.05$, and will be called highly significant if $P < 0.001$.

Results

Targeting performance

Gain

In all conditions the relationships between achieved (D_a) and desired (D_d) displacement obtained from individual Ss were linear or close to linear as illustrated by the example in Fig. 1 (*top panel*) which depicts the result of one subject during passive rotation in darkness (condition V). The example is also typical in that there were no

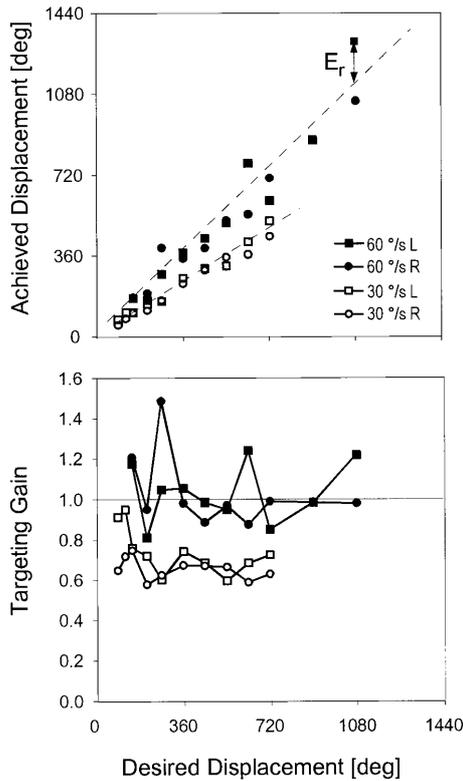


Fig. 1 Example of an individual subject's responses (first series, passive rotation in complete darkness). *Top panel*, achieved displacement (D_a) as a function of desired displacement (D_d); symbols discriminate velocity and direction of platform rotation (L left; R right). *Dashed lines* represent linear fits to data obtained with 30 and 60°/s, respectively. E_r , definition of random error (=deviation of individual trials from linear fit). *Lower panel*, same data represented now in terms of the targeting gain ($G_T = D_a/D_d$); *horizontal line*, ideal value $G_T = 1$

systematic differences between left (squares) and right (circles) turns whereas angular velocity had a clear influence; during slow rotation (open symbols) the subject signalled completion of the desired displacement prematurely ($D_a < D_d$) whereas she achieved the desired rotation almost correctly during fast rotation ($D_a \approx D_d$; filled symbols).

The dependence on velocity becomes particularly evident if the subject's performance is plotted in terms of the targeting gain ($G_T = D_a/D_d$). As depicted in the *lower panel* of Fig. 1, during fast rotation G_T was close to unity in our sample subject, indicating that she perceived her displacement about correctly. In contrast, upon slow rotation G_T reached only values of the order of 0.7, i.e. the subject undershot the desired displacement; note that this *undershoot* betrays an *overestimation* of the actual physical rotation. Note also that G_T , as defined above, may depend on the magnitude of the desired displacement in spite of the fact that the relationship between D_a and D_d is linear. Because this relationship generally has a positive, non-zero intercept with the ordinate, frequently a behaviour similar to that exhibited by the gain curve for 30°/s leftward rotation in Fig. 1 (*lower panel*) is ob-

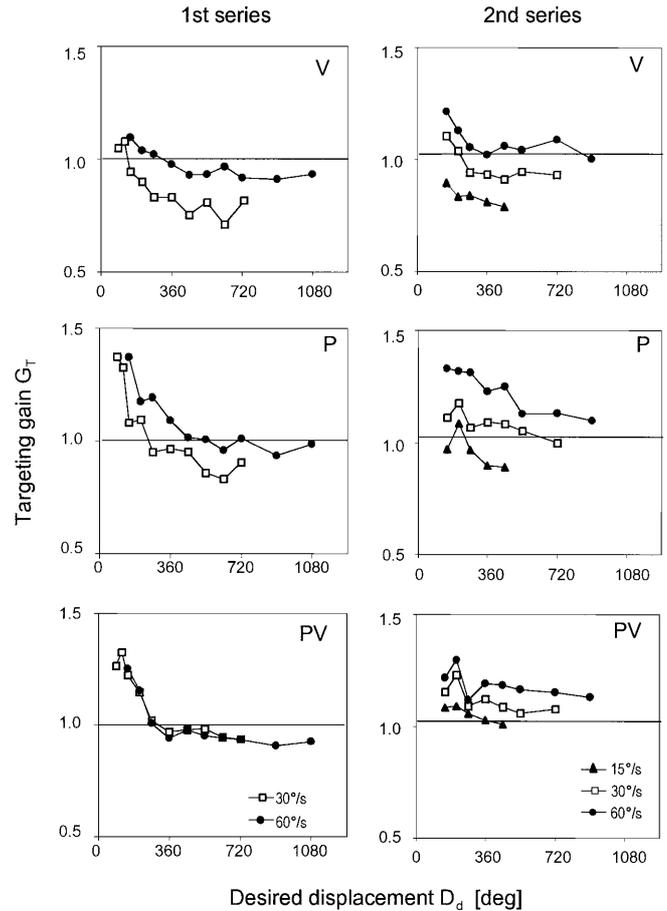


Fig. 2 Population averages of targeting gain as a function of desired displacement. *Left*, results of first series ($n=16$); *right*, second series ($n=12$). Turning modes as labelled by acronyms (V passive rotation, P treadmill stepping, PV active turning). *Symbols* distinguishing turning velocity as explained in *lower panels*

served, which is characterised by a marked increase in gain for small values of D_d .

Figure 2 shows the population averages of the targeting gain for each turning mode and each velocity obtained in the first (*left panels*) and second series (*right*), respectively. Upon comparing G_T across conditions and series, the following consistent qualitative observations can be made:

1. Subjects had a general trend to overshoot when the desired displacement was small ($G_T > 1$; signal button actuated too late) and to be correct ($G_T \approx 1$) or undershoot ($G_T < 1$; signal too early) when large displacements were requested.
2. In the two monomodal conditions (V and P) the targeting gain clearly depended on turning velocity (smaller with slow than with fast rotations), whereas during combined vestibular *and* podokinetic stimulation (active turning, PV) turning velocity had much less effect on targeting gain.
3. On average, the (non-signed) deviations from the ideal gain value $G_T = 1$ were smaller during active turning than in each of the two monomodal conditions.

Table 1 ANOVA of targeting gain and percent random error; main factors *condition* (turning modes V, P and PV), *turning velocity* and *desired displacement* (D_d)

Factor number	Gain						Percent random error					
	First series, $n=16$			Second series, $n=12$			First series, $n=16$			Second series, $n=12$		
	df	F	P	df	F	P	df	F	P	df	F	P
1 (Condition)	2	7.3	0.003*	2	3.3	0.058	2	3.0	0.065	2	18.7	0.000*
2 (Velocity)	1	17.9	0.001*	2	23.8	0.000*	1	0.3	0.616	2	0.8	0.482
3 (D_d)	7	27.1	0.000*	4	8.6	0.000*	7	10.4	0.000*	4	3.4	0.017*
1×2	2	12.8	0.000*	4	2.6	0.048*	2	0.4	0.695	4	1.8	0.138
1×3	14	2.4	0.003*	8	1.9	0.067	14	2.0	0.020*	8	0.6	0.805

* Significant probabilities

The qualitative observations made from Fig. 2 were confirmed by the results of a three-way ANOVA (Table 1). In each of the two series all variables (*turning mode*, *velocity* and *desired displacement*) had highly significant effects upon G_T (except for the factor *turning mode* which was only close to significant in the second series). *Post hoc* analysis indicated that:

1. Gain decreased as a function of D_d and frequently assumed values below unity when large displacements were required, indicating an *overestimation* of the displacement.
2. Gain increased along with turning velocity, indicating an increasing tendency for *underestimation*. Noticeably, however, this increase depended differentially upon the turning mode as witnessed by a significant interaction between factors *turning mode* and *velocity*; *post hoc* analysis showed that significant differences between slow and fast rotations occurred with modes V and P, but not with PV. Thus, during combined vestibular and podokinetic stimulation (PV) the targeting gain depended to a much lesser degree on turning velocity than it did during pure vestibular (V) or pure podokinetic (P) stimulation.
3. Gain was smallest (and mostly <1 , reflecting an *overestimation*) during passive rotation as compared to both active turning and treadmill stepping.

That these characteristics were a common trait of both experimental series was also confirmed by a four-way ANOVA with *series number* (first, second) as independent variable and *turning mode*, *velocity* and *desired displacement* as repeated measurements variables, using a merged data set containing those results of both series that had been obtained with identical velocities and displacements. There was a significant main effect of the series number ($P=0.041$) reflecting the obvious (from Fig. 2) fact that G_T was, on average, larger in the second series. The effects of the repeated measurement variables were all highly significant, thus confirming the results of the separate ANOVAs. Most relevant, however, there were no significant interactions between the series number and the other variables, suggesting a similar dependence of G_T on turning mode, velocity and D_d in both series. The only exception was a significant ($P=0.015$)

double interaction *series number* \times *turning mode* \times *desired displacement* which corresponds to the differential rise of G_T for small values of D_d in conditions P and PV evident from Fig. 2.

Random error

As described in Materials and methods, the random error was defined as the deviation of individual trials from a subject's average behaviour in any given experimental condition, the average being equated to the linear regression of achieved on desired displacement (see *top panel* of Fig. 1). This approach is justified because thorough visual inspection of the data from each subject and each condition had suggested that a linear regression was indeed an appropriate description in the vast majority of the cases (see example in Fig. 1).

In all conditions, the random error likewise increased in an essentially linear way with the magnitude of the desired displacement. The further analysis therefore was carried out in terms of the *percent random error*, defined by $\%E_r = 100\% \cdot E_r / D_f$ (error normalised to linear fit D_f).

The population averages of the percent random error are depicted in Fig. 3 as functions of the desired displacement (*left*, first series; *right*, second series). Because the ANOVA (Table 1) had indicated that in none of the two series turning velocity was a significant factor, these averages represent pooled data from all velocities. The effect of the turning mode upon the random error was highly significant in the second series, but only close to significant in the first one; however, the significant interaction between turning mode and desired displacement evident from Table 1, and inspection of Fig. 3, suggested that at least for large displacements the effect of turning mode reached significance also in the first series. An ANOVA applied to a subset of the data including only displacements $\geq 270^\circ$ confirmed this conjecture (significant effect of turning mode, no interaction with D_d). Finally, as evident from Fig. 3, the percent random error was smallest during active turning. *Post hoc* analyses of the second series indicated that $\%E_r$ was significantly smaller in turning mode PV than it was with either V or P, while for the subset $D_d \geq 270^\circ$ of the first

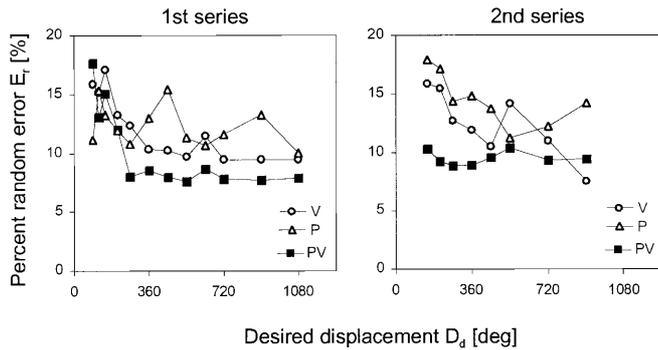


Fig. 3 Percent random error as a function of desired displacement; data pooled across turning velocities. *Left panel*, first series; *right panel*, second series. Turning modes as labelled by acronyms (V passive rotation, P treadmill stepping, PV active turning)

series the difference was significant only with respect to turning mode P.

Subjective reports

Strategies

During passive and active turning (V and PV) a majority of Ss (17 and 18, respectively, out of 28) conceived themselves as being equipped with a pointer sweeping across an imagined “scale” in space, frequently a mental representation of a familiar room or of the previously seen laboratory with corners or walls marking 90° sections. A few Ss preferred to view themselves as carrying a scale (essentially the body scheme) rotating past a pointer aligned with their prerotational position, while others could give no precise account of their strategy. Five Ss confessed that during passive rotation they could not help but ignore the instructions and use *temporal* cues, mostly multiples of the duration of the initially perceived 90° displacements.

In the treadmill mode (P) Ss had been suggested two alternative strategies (see Materials and methods). Most Ss (17 out of 28) considered the *relative* motion between the self and the platform, and of these, 12 focused on the platform rotation under their feet (mostly with an imagined pointer on the platform and a body-fixed scale), while the other 5 invoked the rotation of the self on the platform (one of the latter 5 Ss confessed to have counted steps). Of the remaining 11 Ss, 5 used the metaphor of platform rotation in space, whereas the other 6 could give no precise description. If Ss entered a state of circular vection (see below), they would refer to a body-fixed pointer sweeping through an imagined space.

Perceived velocity and after-rotations

Upon retrospective questioning at the end of condition V, 13 out of 16 Ss (first series) and 8 out of 12 Ss (second series) indicated that they had experienced an always

constant angular velocity; the other Ss either regularly or occasionally felt a slowing during rotations of low velocity and long duration. In the first series, Ss also had been questioned for the occurrence of after-sensations. Four out of these 16 Ss reported occasional counter-rotations, whereas 1 subject felt a continuing rotation.

The velocities of active turning and of platform rotation during treadmill stepping were perceived as being constant by all Ss (sole exception: 1 subject of the second series had experienced an acceleration of the platform). Occasional after-sensations following active turning were noted by 4 Ss out of 16 (counter-rotation, 3 Ss; continuing rotation, 1 subject). No after-sensations were reported after treadmill stepping.

Vection

Towards the end of “long-distance” treadmill stepping 2 out of 16 Ss in the first series and 5 out of 12 Ss in the second series occasionally experienced an illusion of turning in space counter to the direction of platform rotation (podokinetic circular vection, also called “apparent stepping around”, Bles 1981). All other Ss reported that they felt stable in space, in accordance with the mental set established by the experimenter’s explanations and instructions.

Retrospective subjective ranking of task difficulty (first series)

According to the rankings collected after completion of all three conditions 11 Ss (out of 16) considered active turning as the easiest condition and only 1 subject thought it was the most difficult one. Half of the Ss ranked passive rotation as most difficult and none considered it as easiest condition. Treadmill stepping gave rise to fairly non-uniform judgements; while 7 Ss thought it was the most difficult condition, 3 found it to be the easiest one.

Confidence scores (first series)

In all conditions and all Ss the school marks delivered after each single trial to score Ss’ confidence into their performance varied considerably from one trial to the next. Within a given condition there was no correlation whatsoever between these variations and either G_T or E_T ; thus, an almost perfect performance could be associated with a very poor school mark, and vice versa. However, averaged across trials and Ss, these marks exhibited a significant dependence on the experimental condition and on the magnitude of the desired displacement (highly significant) whereas the effect of velocity was not significant (three-way ANOVA). Noticeably, confidence into own performance was best in the active turning mode (PV). With all turning modes there was a confidence

maximum if displacements of 360° (full turn) were requested.

Retrospective scoring of task difficulty and self-confidence (second series)

Targeting was considered to be easiest during active turning, passive rotation ranked intermediate and treadmill stepping worst (the difference between PV and P was significant, whereas that between PV and V was not). Likewise, self-confidence as to the correct performance of the task was better during active turning than during either passive rotation or treadmill stepping (which scored similarly), but none of these differences reached statistical significance.

Discussion

In the present experiments we have compared the perceptions of angular displacement by human Ss in three different situations; in two of these situations only a single sensory cue was available (either vestibular or podokinesthetic) while in the third condition Ss had access to both cues. We wished to learn from these experiments whether, with *both* cues available, perception would correspond to a weighted average of the perceptions arising with either cue alone.

As detailed in the Introduction, several authors already have made quantitative comparisons between the perceptions of angular displacement during passive rotation (vestibular cue only) and active turning (vestibular and podokinesthetic cues combined), using mostly Ss' accuracy in a targeting task as an indicator of this perception (Bles 1981; Yardley and Higgins 1998; Bakker et al. 1999; Jürgens et al. 1999; Marlinsky 1999). A consistent finding in these experiments was a reduction of Ss' variable error during combined vestibular *and* podokinesthetic stimulation as compared to vestibular stimulation alone. This result can be interpreted in two different ways: Either the vestibular (*ves*) and podokinesthetic (*pod*) cues are affected by about equal noise levels which, upon combination of these cues during active turning, are attenuated by an averaging process, or the podokinesthetic cue is of inherently superior quality in terms of noise and takes precedence over the vestibular signal during active turning. Clearly, to answer this key question one has to study the characteristics of the podokinesthetic cue in isolation; to this end we resorted to the treadmill paradigm in which Ss (almost) remain stationary in space and therefore can only refer to *pod* (for possible complications from high-frequency vestibular signals at the pace of stepping, see below). To our knowledge, so far only Bles (1981) has attempted to quantify the perception arising during circular stepping on a treadmill. His measurements essentially were limited to a single condition involving 18 full turns of the treadmill at 60°/s. Thus, the present report appears to be the first quantitative account

of angular displacement perception during circular treadmill stepping covering a broad range of amplitudes (90–1080°) and different velocities (15, 30 and 60°/s). In the realm of linear locomotion analogous investigations have been carried out by Mittelstaedt and Glasauer (1992) and Mittelstaedt and Mittelstaedt (2001).

In the following, before focusing on the main topic of this study, we shall first consider the cognitive processes that presumably are responsible for the results obtained with pure vestibular stimulation and will briefly describe a model (explained in more detail in the Appendix) formalising our pertinent hypotheses. This “detour” is indicated because these processes also bear on the question, to be asked subsequently, as to how far the observations made during active turning support the notion of cue averaging. We will examine this question by analysing in turn the percent random error and the targeting gain. Because it will turn out that the characteristics of these parameters do support the averaging hypothesis only partially, at best, we then will ponder alternative hypotheses to explain our results and specifically discuss the possibility that a scheme based on a vestibular “*eigenmodel*” might account for our observations. Finally, we shall examine the degree to which auxiliary cues gained by intentionally or unintentionally ignoring the instructions may have influenced the results.

Effect of turning velocity on vestibular targeting: a hint at cognitive processes

The peripheral vestibular system has high-pass characteristics with a time constant (τ) of about 5 s. This value is thought to be improved by central mechanisms to yield a behavioural value of $\tau=16-20$ s (Guedry 1974; Young 1981; Mergner et al. 1996). As already pointed out in a previous study (Jürgens et al. 1999), given these values, one would expect an increasing *underestimation* of passive displacements as turning velocity is lowered and as duration is prolonged. Correspondingly, targeting gain should markedly increase beyond unity when turning velocity is low and when large displacements are to be achieved. Our observations do in no way conform to these predictions: in both series, G_T decreased (i.e. self-displacement was *overestimated*) when turning velocity was lowered and when the magnitude of D_d was raised (Fig. 2, *panels V*). An overestimation of passive angular self-displacement during targeting also has been reported by other authors (see, for example, Ivanenko et al. 1997; Bakker et al. 1999) albeit without specification of the effect of turning velocity.

Overestimation of self-displacement in spite of a fading vestibular signal is a phenomenon that also occurs during passive *linear* motion (see, for example, Mittelstaedt and Glasauer 1991; Israël et al. 1997; Mittelstaedt and Mittelstaedt 2001). In particular, the findings of Mittelstaedt and collaborators closely parallel the present ones in that they also reveal a decrease of G_T for small stimulus velocities and large displacements. As

an explanatory model these authors consider a leaky integrator which initially is charged with a representation of the target distance. This integrator then would be discharged by a signal of otolith origin that is assumed to veridically reflect the velocity of the ongoing displacement; once the integrator has been completely discharged the subject would feel on target. For several reasons, this model is not applicable to the present data.

In the first place, the model is difficult to reconcile with the fact that our Ss could store the desired displacement in symbolic terms and could monitor their self-displacement by counting 90° partitions according to their body scheme. Secondly, it is also not applicable for formal reasons. Indeed, in the leaky integrator model the spontaneous decay of the integrator occurs along a stereotyped exponential that is only a function of time (t) irrespective of stimulus velocity. Accordingly, when G_T is considered as a function of t rather than of D_d , all values should fall on a single curve reflecting the spontaneous discharge of the integrator. This prediction does not bear out with the present results since plots of $G_T=f(t)$ still show a clear dependence on stimulus velocity. The reader can appreciate this fact by noting that the curves of $G_T=f(D_d)$ for 60°/s in the *top panels* of Fig. 2 cannot be matched to those for 30°/s (or 15°/s) through compression by a factor of 2 (or 4) along the abscissa.

To explain the observed performance during vestibular targeting, we hypothesise that Ss tacitly proceeded from the notion of a rotation at constant velocity although the instructions contained no hint at the velocity profile of the stimuli (except for condition PV in the first series where Ss were told to turn at a constant velocity). In accordance with this presumed scenario, they must have unconsciously ignored the fading of the vestibular cue during slow and long-lasting rotations, filling in a “virtual” perception, and this virtual perception would perpetuate, by extrapolation, the “real” perception evoked during the initial part of the rotation. Such an interpretation of Ss’ behaviour is supported by the finding that, even upon explicit questioning at the end of sessions with turning mode V, most Ss denied to have perceived a slowing of self-rotation, and that Ss also rarely experienced a feeling of counter-rotation at the end of a V stimulus. Apparently, the suprathreshold vestibular cue that must have arisen when the platform stopped at the end of a trial, mostly was interpreted in a natural way as a signal to end the internally maintained percept of an ongoing constant rotation.

The use, by our Ss, of an internal construct that is no longer supported by a real cue is well illustrated by the occasional occurrence of a perceptual ambiguity which Ss described in about the following terms: “I was rotating at constant speed all the time, yet at some moment I had the impression that nothing more happened”. These Ss apparently had two coexisting sensations, one of a decreasing turning *intensity* paralleling the fading of the vestibular afferents, and a second one indicating a continuing accumulation of displacement at a constant rate, kept alive by the putative mechanism of extrapolation.

Interestingly, a conceivably similar dissociation between a decaying perception of intensity and an ongoing perception of displacement has been observed by Brandt and Dichgans (1972) in the aftermath of optokinetic stimulation.

Extrapolation, taken per se, can only explain why G_T does not rapidly increase for large values of D_d as it would if vestibular navigation performance was limited by a time constant of 20 s. Two further assumptions are necessary to account for (1) its dependence on velocity and (2) its increase for small values of D_d :

1. The extrapolation is biased toward a default velocity (v_d) by Ss’ expectation from previous experience, but also by guessing, preferences and other higher cognitive functions; conceivably, v_d has a value corresponding to the middle or low range of the velocities occurring in an experiment. The resulting undervaluation of large, and overvaluation of low, velocities can be viewed as an example of the “range effect” (Poulton 1977; sometimes also called “contraction bias”, Poulton 1981) which is known to affect many perceptual and psychomotor performances.
2. For Ss to feel on target, the displacement dead-reckoned by integration of the extrapolated velocity must exceed the desired value by some fixed amount, conceivably because this comparison between the two displacement signals is affected by noise.

In the Appendix we present a formal description of these assumptions and hypotheses in terms of a model (Fig. 6). Basically, this model performs three operations:

1. The extrapolation proper which provides for an essentially veridical reconstruction (v_r) of the physical velocity (V) throughout the time of platform rotation (note that the leaky integrator model implicitly requires a similar operation as it assumes a non-decaying, veridical velocity signal at the input of the leaky integrator).
2. A distortion of the reconstructed velocity in favour of a default value (v_d) such that the perceived velocity (v_p) becomes

$$v_p = G_0 \{ w \cdot v_r + (1 - w) \cdot v_d \},$$

where w is a weight factor ($w < 1$) and G_0 a gain factor accounting for the global tendency towards overestimation ($G_0 > 1$).

3. The integration of v_p yielding a dead-reckoned value of current displacement (D_p) which then is compared to $D_d + \Delta$, where Δ is a fixed threshold.

With these model assumptions the targeting gain can be expressed by

$$G_T = V/v_p \cdot (1 + \Delta/D_d) \quad (1)$$

As shown in the Appendix, Eq. (1) can be fitted fairly well to the experimental data; in particular, it provides a definitely better fit than the leaky integrator model because it explicitly takes into account the effect of turning velocity.

We point out that Eq. (1) and the underlying model are mainly meant to mould the verbal conjectures at the beginning of this section into a form that allows us to use them below as a “building block” when we consider a possible model of vestibular-podokinesthetic *fusion* (see “An interpretation in terms of the vestibular “*eigenmodel*” concept”); note that the model is non-optimal in that it has not been designed to provide the most parsimonious description of our results.

As an important consequence, the presumed filling in for the decaying peripheral vestibular signal renders the vestibular frequency response comparable to that of the podokinesthetic system, as witnessed by the general similarity of the G_T curves obtained in conditions V and P (Fig. 2). It thus *a posteriori* legitimates our posing the question of vestibular-podokinesthetic fusion which, otherwise, would have made sense only for high frequency stimuli, i.e. for displacements of short duration during which the peripheral vestibular signal remains “alive”.

Our present finding of a dependence of G_T on angular velocity is at conflict with a previous study (Jürgens et al. 1999) where we had found the perception of self-displacement during passive rotation to be independent of the turning velocity. A control experiment performed to resolve this conflict suggests that our previous inability to demonstrate an effect of velocity with the methods of verbal estimation or self-steering of the platform towards a target appears to result from both a larger variability (approximately 19%) in comparison to the presently used paradigm ($\leq 13\%$) and different mental sets associated with these procedures.

Differences in mental set and in the focus of Ss’ attention must also be invoked to explain why our results, and those of others concerned with navigation (cf. above), are at variance with the findings of earlier investigators who predominantly were interested in quantifying the sensation of turning *velocity* (and who actually may have measured the perceived *intensity* of rotation, i.e. a compound of angular acceleration and velocity; cf. Benson and Brown 1992; Becker et al. 2000). Although these measurements frequently were made via the round-about of repeated displacement estimations, the reported results were indicative of a perceptual time constant of the order of 10–20 s only (for a review see Guedry 1974). Conceivably, some of these findings result from an “overinstruction” of the Ss, motivated by the expectation, on the part of the experimenters, of shorter time constants than naive Ss actually exhibit; significantly, Guedry (ibid.) points out “... some observers respond with an apparently autogeneous rate.... it is difficult to specify the kind and amount of instruction necessary to obtain what appears to be reasonable results...”.

Random error: why is it minimal during active turning?

We now turn to our main topic, to wit the question whether the *ves* and *pod* information about self-turning is

averaged during active stepping around, or whether *ves*, being conceivably more noisy than *pod*, is more or less ignored in the active mode. We here first shall examine the evidence from the random error.

Weighted averaging is an obvious way to combine two independent, noise-affected sources of information concerning the same event. As already explained in the Introduction, if the source having smaller noise is weighted more heavily, such an average is, in terms of noise, the optimal information about the event that can be obtained. If we assume, for the time being, that during active turning *ves* and *pod* are indeed combined in this way, we can answer our key question by determining the variability of *pod* in relation to that of *ves*. If this variability is substantially lower, *pod* will be weighted more heavily than *ves* upon combination, i.e. *pod* will take precedence over *ves*. In that case, the previously reported lower variability during active as compared to passive rotation would essentially reflect the characteristics of *pod*. On the other hand, if both cues have about similar variability, they will be combined with equal weights, and the lower variability during combined stimulation then would reflect the noise attenuation, by a factor of about $1/\sqrt{2}$, resulting from equal-weights averaging.

Both experimental series unequivocally indicate that during monomodal podokinesthetic stimulation (treadmill stepping) the percent random error was of the same order of magnitude as during pure vestibular stimulation (it actually was even slightly larger) and, by the same token, significantly larger than during the combined stimulation (except for the case of the smallest displacements in the first series). Hence, the reduced variability during active turning would seem to result from the *combination* of *pod* and *ves* rather than from an inherently lower variability of *pod*.

Yet, below we will question this seemingly straightforward conclusion because it is not fully supported by the observed characteristics of the targeting gain and because of the possibility that Ss’ perception during treadmill stepping might be affected by additional factors that do not apply to the active situation.

Targeting gain: to which degree is it compatible with the notion of cue averaging?

We now shall ask whether and to which degree the behaviour of the targeting gain supports the notion of cue averaging. Based on the observation that the random errors in conditions V and P are of the same order of magnitude, we can postulate that if *pod* and *ves* are indeed averaged, they so are with about equal weights. Accordingly, the targeting gain recorded during active turning, $G_T(PV)$, should approximately equal the average of the gains obtained in the two monomodal situations, $G_T(P)$ and $G_T(V)$. However, by this criterion, the measured values of G_T are only *partially* compatible with the notion of an equal-weights averaging. This is illustrated in Fig. 4 which tests the averaging hypothesis separately

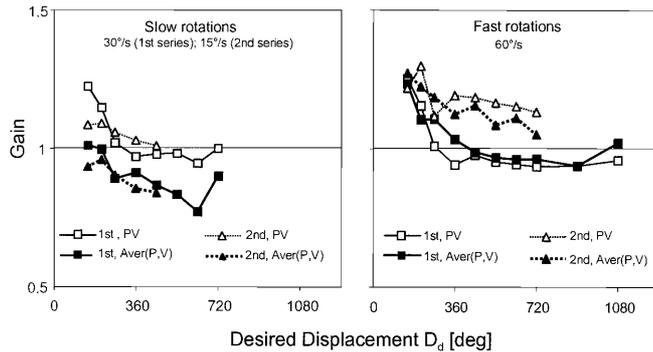


Fig. 4 Comparison of targeting gain during active turning (*open symbols* labelled “PV”) with average of gains obtained during passive rotation and treadmill stepping, respectively [*filled symbols* labelled “Aver(P, V)”]. *Left panel*, slow rotations (30°/s in first series, 15°/s in second); in both experimental series (labelled *1st* and *2nd*), Aver(P, V) was significantly smaller than PV. *Right panel*, fast rotations (60°/s); in both series Aver(P, V) and PV were similar

for fast and slow rotations. According to the *right panel* of Fig. 4, upon fast rotation, the *average* of the targeting gains recorded in the vestibular and podokinesthetic conditions (*filled symbols*) closely matched the gain obtained during active turning (*open symbols*). On the other hand, as shown in the *left panel*, upon slow rotation, this average always was significantly smaller than the gain obtained in condition PV [$P < 0.001$, three-way ANOVA with factors $mode = [PV, Average(P,V)]$, $velocity$ and $desired\ displacement$, followed by a *post hoc* Scheffé test}. Thus, the behaviour of the targeting gain is compatible with the notion that cue averaging takes place during fast turning, but not during slow turning.

Possibly, the deviant behaviour during slow turning is related to the filling in of an extrapolation for the fading vestibular signal postulated above. Such a replacement of the fading vestibular signal by an internal construct might occur only if no other cues are available. Consequently, during *slow* active turning, when the vestibular afferents rapidly drop below threshold, the vestibular perception would not be artificially perpetuated but simply discarded because Ss could draw on the permanently available podokinesthetic signal. On the other hand, during *fast* active rotations, averaging would take place because the vestibular signal is vigorous enough to entertain a “real” vestibular percept within the range of time epochs occurring in our experiments.

In summary, both the random error and the targeting gain seemingly concur to suggest that during fast active turnings two cues of similar variability, *ves* and *pod*, are averaged resulting in a perception of angular self-displacement that is less variable than the perceptions evoked by either cue alone. However, the evidence for slow rotations is conflicting; whereas the random error is compatible with the assumption of a combination of *ves* and *pod* by averaging, the targeting gain is not. Therefore, in the following we shall explore alternative explanations for our results, including the option that actually no averaging takes place at all.

Complications of the averaging hypothesis: search for alternative explanations

The above hypothesis of a fusion mechanism that averages only real, but not virtual, perceptions and that, therefore, would be invoked only during fast active turning has several flaws:

1. In all trials the vestibular signals arising during the onset of passive or active rotations were far above the perceptual threshold ($< 2.4^\circ/s^2$, Mergner et al. 1991; $< 1.2^\circ/s$, Kolev et al. 1996); for passive rotations the initial peak acceleration was adjusted to about $100^\circ/s^2$ independent of the subsequent cruising velocity, and the onset of active rotations usually was even more abrupt. Therefore, during the first seconds of a trial Ss could largely rely on “real” rather than “virtual” perceptions. Accordingly, as long as only *small* (and hence short) active displacements were requested, *ves* and *pod* should have been averaged irrespective of the velocity. The data from low velocity trials shown in the *left panel* of Fig. 4 do not support this expectation; the offset between the calculated averages and the G_T values observed in turning mode PV is about the same for all values of D_d instead of vanishing for small displacements.
2. It was a consistent finding that the dependence of the gain on velocity was lowest during active turning (compare the vertical separation of the G_T curves according to velocity in *panels PV* of Fig. 2 with those in the corresponding *panels V* and *P*). The hypothesised exclusion of the *ves* extrapolation from averaging during low-velocity active turning could be one factor reducing the effect of velocity as it would prevent the virtual percept’s overestimation of slow turnings from influencing performance. According to this explanation, $G_T(PV)$ and $G_T(P)$ should be similar at low velocities. Yet, the data from both experimental series indicate that $G_T(PV)$ actually was larger than $G_T(P)$. Although these differences were not significant from a statistical point of view, their similar occurrence in both series fosters the suspicion that still other factors contribute to achieve a minimal dependence of displacement perception on velocity during active turning.

Taken together, these considerations call for a critical examination of two tacit assumptions upon which all of the preceding discussion rests. We have assumed: (1) that the podokinesthetic signals generated during treadmill stepping and active turning are similar and (2) that in both situations these signals also are perceptually interpreted in a similar way with regard to the achieved angular displacement.

The first assumption could be violated, for example, because Ss might have used different step widths and frequencies during turning modes P and PV. This could differentially influence perceived displacement since, at least for linear displacements, Ss appear to base their displacement estimates preferentially on either step

length or step frequency (Mittelstaedt and Glasauer 1992). We have made no direct measurements of the frequency or the angular magnitude of Ss' steps. However, in most Ss the modulation of the recorded head movements at the pace of their stepping made it possible to infer their mean stepping frequency from the power spectra of these movements. This analysis suggests that Ss used identical stepping patterns during turning modes P and PV: the individual means from the two modes were clearly correlated and the mean frequencies were very similar in both modes (values for 15, 30, and 60°/s: P, 0.44, 0.59, and 0.81 Hz; PV, 0.46, 0.68, and 0.81 Hz). Thus, we have no arguments to invalidate the first assumption.

In contrast, it is much more difficult to maintain the second assumption (similar perceptual interpretation of *pod* during P and PV). Treadmill stepping was by far the most uncommon of the three turning modes. In contrast to Bles' experiments (Bles 1981) our Ss rarely entered a state of circularvection where they would experience the platform as being stationary and the self as turning in space. Accordingly, they had to estimate the *relative* angular displacement between the self and the platform (or vice versa), or the platform's displacement in space; and neither task is facilitated by daily life experience. These circumstances could have caused an artificial enlargement of performance variability that does not reflect the true, inherent quality of the podokinesthetic cue which would surface only if stepping was associated with a sensation of a real rotation *in space*. Such a scenario obviously would invalidate all arguments in favour of cue averaging based on the comparison between % $E_r(P)$ and % $E_r(PV)$. It is difficult to convincingly refute this scenario although the retrospective interviews of our Ss do not hint at a particular difficulty of the treadmill task: the Ss of the first series rated treadmill stepping as no more difficult than passive turning although the latter situation is experienced much more frequently (vehicles, rotating office chairs, etc), and there were three Ss who even thought it was easier than active turning. Likewise, in the second series there was no significant difference between the retrospective school marks for task difficulty during turning modes V and P.

Similar to this caveat concerning the random error, the lack of a compelling perception of rotation *in space* during treadmill stepping also may have had consequences for the targeting gain. For example, the velocity dependence of G_T observed during treadmill stepping might not reflect an inherent property of the isolated podokinesthetic signal but owe to cognitive guessing strategies into which Ss might have been enticed by the unfamiliarity of the situation. Possibly, only the sensation of *true* turning might open access to a reliable, velocity-independent calibration established by the daily-life experience of moving on *firm* ground. Consequently, the low dependence on velocity during active turning would not result from an improvement brought about by sensory fusion but would reflect the intrinsic properties

of the podokinesthetic system, free of distortions related to the lack of a convincing sensation of rotation in *space* during treadmill stepping.

Thus, after having shown that simple, average-based fusion mechanisms can account only partially for the observed targeting behaviour, a critical evaluation of the tacit assumptions underlying the averaging hypothesis (perceptual equivalence of the podokinesthetic cue during treadmill stepping and active turning) leads us to acknowledge the possibility of other forms of interaction between *pod* and *ves*. In the following section we shall show that many, though not all, aspects of our experimental observations appear to fit with an already existing model of vestibular-proprioceptive interaction.

An interpretation in terms of the vestibular "eigenmodel" concept: the importance of evaluating the dynamic state of the body support

Proceeding from an investigation of the role of vestibular and neck-proprioceptive afferents for the perceptions of self-rotation and object motion, Mergner and collaborators (see, for example, Mergner et al. 1991, 1997) have posited a general principle underlying the combination of vestibular and axial proprioceptive afferents. Figure 5 illustrates this principle in a way that anticipates our conclusion that it might account for many of the present findings. According to this principle, the first step in determining self-rotation is to estimate the dynamic state of the body support (the platform in our case). To this end, the proprioceptive afferents, which are thought to be intrinsically "ideal" (no frequency or time dependence), first are transformed by a "vestibular eigenmodel" to confer them the non-ideal characteristics (high-pass) of the vestibular signal. Thus, as illustrated in Fig. 5 for the case of treadmill stepping, *pod* is transformed into a "distorted" cue pod^T which, in response to the sudden onset of a constant-velocity rotation, exhibits the same decaying behaviour as the vestibular cue. The transformed proprioceptive cue then is subtracted from *ves* yielding a difference signal that will equal zero as long as the inputs of the vestibular and the proprioceptive channels are equal; this condition is met if the support is stationary. The difference signal ($v-p^T$ in Fig. 5) therefore is a reliable indicator of support *stationarity* irrespective of how trunk and head rotate with respect to the support (fast or slow, briefly or quasi-permanently; it may not correctly render slow *movements* of the support, though). In a second step (ignoring the "Recover" block for the moment), the original (hence undistorted) proprioceptive afferents (*pod* in the present case, representing body-on-platform velocity v_{BP}) are added to this difference creating a signal of angular body velocity in space ($v_{BS}=v_{BP}+v_{PS}$) which, by integration, ultimately is converted into a perception of angular body displacement in space (D_{BS}). As long as the support is stationary this perception will be determined solely by the proprioceptive signal (because $v-p^T$ and, hence, v_{PS} vanish in

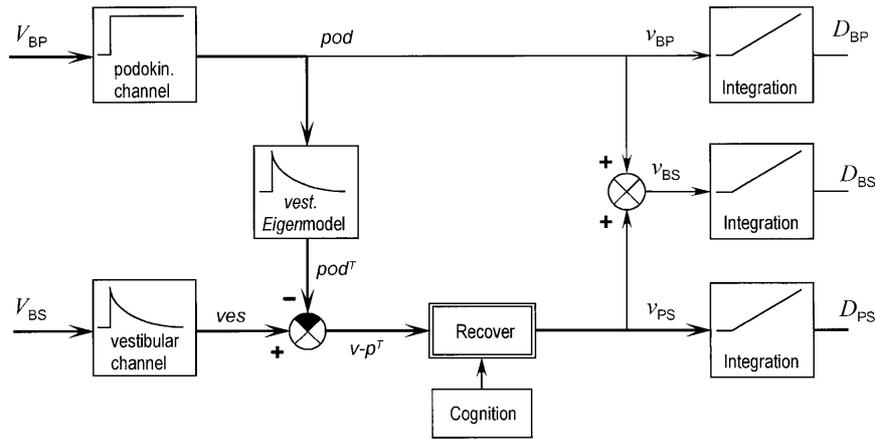


Fig. 5 Principle of vestibular-proprioceptive interaction based on an “*eigenmodel*” of the vestibular channel (Mergner et al. 1991), adapted to the case of vestibular-podokinesthetic interaction during angular navigation. Pathways involved in determining the dynamic state of the support (i.e. of the platform) are outlined by *bold lines*. Transfer characteristics of the vestibular and podokinesthetic channels and of the vestibular *eigenmodel* are symbolised by their step responses. Subscripts $_{BP}$, $_{BS}$, and $_{PS}$ refer to rotations of body versus platform, body in space and platform in space, respectively. V Physical velocities, v central representations of velocities, D displacement perceptions, ves vestibular cue, pod podokinesthetic cue, pod^T transform of pod after the model of the vestibular channel, $v-p^T$ difference $ves-pod^T$; note that $v-p^T$ equals zero if the observer steps around on firm ground. “Recover” and “Cognition” symbolise the cognitive processes that fill in for the fading ves or pod^T signal during navigation (details in Fig. 6). “Integration” represents the conversion of velocity representations into perceptions of angular displacement. Subjects feel on target when the displacement perception reaches D_d plus a threshold value (Δ , compare Fig. 6)

this situation) and, therefore, it will not be affected by the vestibular system’s imperfections (i.e. the processing is optimised for movements on firm ground).

Our observation, made in both experimental series, that the gain curves obtained during treadmill stepping are very similar to those collected during passive rotation in terms of their dependence on velocity (compare panels V and P of Fig. 2) suggests the intriguing possibility that the *eigenmodel* concept may indeed apply to the present data. According to this concept, the velocity dependence of G_T in the treadmill mode would reflect the “purposeful” distortion of pod after the model of ves , which confers the two cues similar characteristics. Specifically, we suggest that the aforementioned mechanism filling in for the decaying vestibular signal (see “Effect of turning velocity on vestibular targeting” and Appendix) actually is not restricted to the vestibular pathway but operates on $v-p^T$, the difference between ves and the transformed pod signal. Accordingly, block “Recover”, which represents this mechanism, is shown inserted into the $v-p^T$ pathway in Fig. 5. Thus, during treadmill stepping when $v-p^T = -pod^T$, pod^T would undergo exactly the same “recovery” procedure as ves does in the case of pure passive rotation. This similar treatment of the vestibular and podokinesthetic cues during turning modes V

and P, respectively, ultimately would lead to the similar dependence of $G_T(V)$ and $G_T(P)$ on velocity.

On the other hand, because of the similarity between ves and the transformed pod signal, $v-p^T$ will become zero during *active* turning and the recovery mechanism therefore will attempt no extrapolation, i.e. it will correctly signal zero platform velocity (see Appendix). Accordingly, the platform will be correctly perceived as being stationary. Perceived self-rotation in space (D_{BS} in Fig. 5) then would be exclusively determined by the original pod cue which, according to our assumptions, has little or no dependency on turning velocity. Thus, the model not only accounts for the similar effect of the turning velocity on $G_T(V)$ and $G_T(P)$, but also for its little influence on $G_T(PV)$, the targeting gain measured during active turning.

The *eigenmodel* scheme also offers a hypothetical explanation for why the random error was minimal in mode PV. Indeed, as detailed in the Appendix, the velocity signal recovered by extrapolation of the fading vestibular signal (or of $v-p^T$ if the scheme in Fig. 5 is correct) has to pass a threshold which prevents low-frequency noise from influencing the subsequent velocity-to-position conversion, and such noise conceivably could result from the recovery process. This noise suppression works most effectively during active turning when $v-p^T$ is close to zero and therefore cannot cross the threshold. The variability of targeting performance then would be mainly determined by the intrinsic properties of the original, undistorted pod cue. On the other hand, the non-zero velocity signals arising during passive rotation and treadmill stepping would carry the noise across the threshold, thus accounting for the larger variability of the results obtained with the monomodal conditions V and P (for a similar discussion of the noise predicted by the *eigenmodel* scheme see Mergner et al. 2001).

Finally, note that the *eigenmodel* scheme does not address the observation that in all conditions, monomodal or bimodal, G_T was larger when small displacements were requested as compared to large ones (Fig. 2). To account for this observation, we generalise the explanation suggested in the context of vestibular targeting to all conditions, i.e. we assume that Ss signal their being on target once the currently perceived displacement (D_p) equals $D_d + \Delta$ holds.

Although the above interpretation of our observations in terms of the *eigenmodel* concept is appealing and more comprehensive than the straightforward averaging hypothesis, it is also not without problems: it rests on the tacit assumption that the targeting performance observed during treadmill stepping reflects D_{PS} (see Fig. 5), i.e. Ss' estimate of platform rotation in space. Yet, according to the retrospective interviews, most of our Ss concentrated on the perception of *relative* body-to-platform displacement (D_{BP}) rather than on platform rotation in space. However, *relative* displacements between body segments, and between the body and its support, are thought to be determined exclusively by the *original* proprioceptive cue in the *eigenmodel* scenario (accordingly, in Fig. 5, D_{BP} is shown to depend only on *pod*); consequently, they would not exhibit the observed dependence on velocity which arises only in the process of redressing the transformed version of *pod*. It is interesting to note, therefore, that the five of our Ss who reportedly based their targeting on the perception of platform rotation in space did not differ from the remaining Ss with regard to their targeting gain during treadmill stepping. Possibly, therefore, Ss who thought to have focused on the self-to-platform rotation, in reality also based their targeting behaviour on the platform-in-space rotation. Clearly, future experiments along the same lines will have to more rigorously focus Ss' attention on exactly one type of perception such that Ss' responses can be unambiguously assigned to the signals postulated by the vestibular *eigenmodel* scheme (D_{BP} or D_{PS} ; Fig. 5).

Role of non-solicited cues and strategies

In both the active and passive turning modes the vestibular signal related to the cruising velocity disappears because of the vestibular system's high-pass characteristics. However the two modes differ in that during active turning there is also a permanent vestibular high-frequency signal at the pace of the Ss' stepping. Could this signal in some unexpected way have contributed to the better targeting performance in the active mode? We have explored this possibility in a supplementary experiment using a variant of condition V in which an oscillatory component mimicking the step correlated modulation of turning velocity was superimposed on the constant velocity profile (1.6 Hz, effective head amplitude about 80% of the constant component). With low velocity rotation (30°/s), this procedure significantly increased the targeting gain from an average of 0.8 (a 20% undershoot) to almost unity, whereas the percent random error did not change [three-way ANOVA with factors *condition*=(non-oscillating/oscillating), *velocity*=(30, 60°/s) and *desired displacement*=(150,..., 720°) followed by a *post hoc* Scheffé test]. It would be a premature conclusion, however, to ascribe the improvement of the targeting gain to a direct effect of the vestibular modulation upon perception. Rather, the retrospective reports of some Ss suggest that they more or less involuntarily used a strategy of counting the number of oscillation periods.

Covert or even overt counting, either in the form of step counting or of counting time units, occasionally also occurred in the main experiments as witnessed by the retrospective reports of some of our Ss. Thus, counting is likely to have been one factor contributing to the extrapolation of displacement perception during long-lasting vestibular stimulation as well as to recording displacement during active turning and treadmill stepping. This intrusion of intelligent behaviour appears to be virtually unavoidable in experiments with humans and must be considered an integral part of the mechanisms for spatial orientation. However, it is important to note that it does neither invalidate our question as to the role of sensory fusion nor the answers collected in the present experiments. Indeed, in order to correctly associate a time lapse or a step with the angular displacement achieved during this time, or by means of this step, these counting units must be calibrated by sensory information. For example, during passive rotation Ss must have "listened" to their vestibular afferents to determine the first or the first two quarter turns before they could build a temporal metaphor of displacement magnitude to further guide their targeting. Moreover, if conscious or subconscious step counting played a role in treadmill stepping, it is an almost semantic question only whether the recording of individual steps is an auxiliary strategy or whether it represents a direct translation of the arising discontinuous "chunks" of proprioceptive and efferent information into a notion of displacement. In fact, given the step magnitudes are available, step counting can be considered as a form of spatial integration that would be the functional equivalent of the velocity-to-displacement integration that must occur in the vestibular pathway. Thus, contrary to the assumptions of Fig. 5, *pod* might not be a velocity-coding signal at all but might always signal displacement increments. Yet, with a few minor changes, the scheme in Fig. 5 still would seem to be appropriate. Basically, (1) the temporal integrator in the v_{BP} pathway would be replaced by a line integration of the *pod* increments, (2) the summing junction $v_{PS}+v_{BP}$ would be moved behind the integrators such that $D_{BS}=D_{PS}+D_{BP}$ and (3) a differentiation would be added to the vestibular *eigenmodel* (or there exists a second, intrinsically velocity coding type of podokinesthetic afferents).

Conclusion

Taken together, the evidence from the gain and the random error observed in the present targeting task is partially compatible with the notion of cue averaging which would mainly apply to fast rotations; however, it also could reflect other scenarios in which the full quality of the podokinesthetic information only can be exploited if associated with a sensation of *real* rotation with respect to space. Inasmuch as the development of such a sensation initially requires the presence of a vestibular signal, or the balancing between a vestibular and a distorted proprioceptive signal (as in the vestibular *eigenmodel*

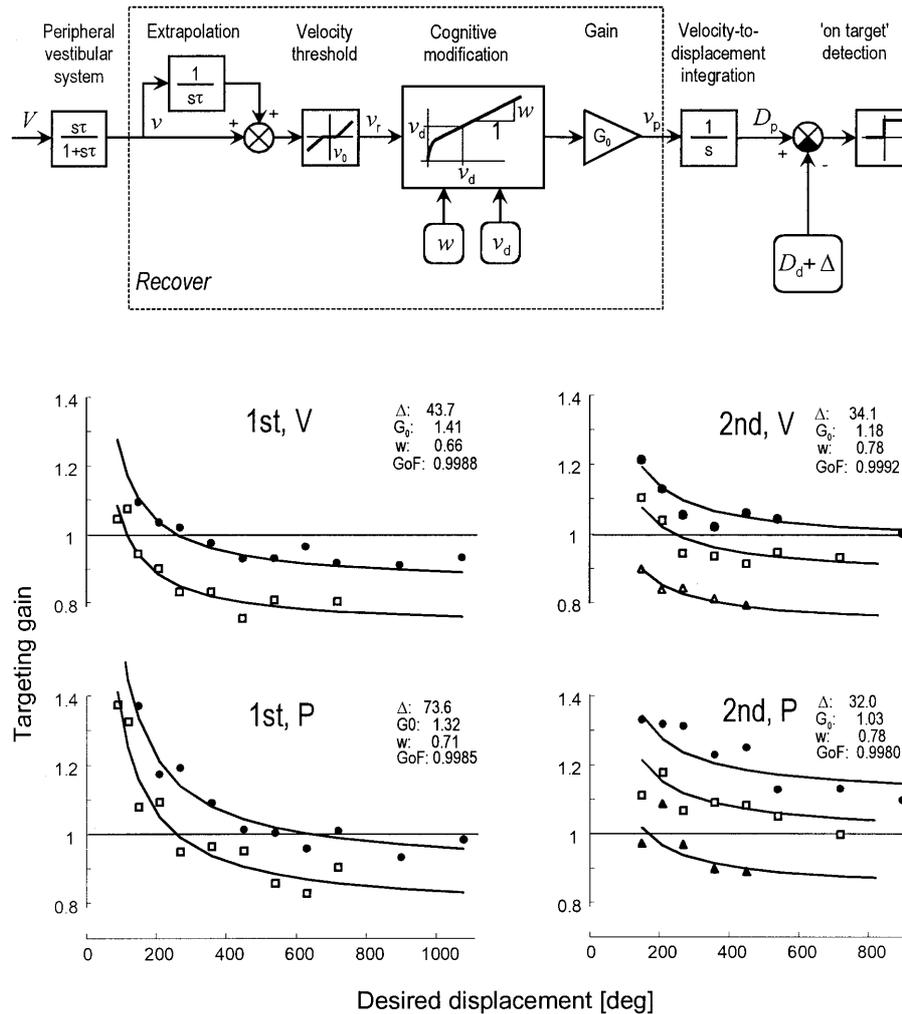


Fig. 6 Model formalising the hypotheses put forward to explain: (1) the extrapolation of the fading vestibular velocity signal and (2) the non-linear characteristics of the vestibular targeting gain. Linear elements are specified by their transfer functions in Laplace notation, non-linear elements by their output-versus-input functions. Elements inside *dashed outline* correspond to block “Recover” in Fig. 5. Therefore, in a more general sense, the model is concerned with the extrapolation of $v-p^T$, the internal estimate of platform angular velocity $V (=V_{BS}-V_{BP}$ in terms of Fig. 5). v , fading velocity signal ($=v-p^T$ in Fig. 5); v_0 , threshold (1.2°/s); v_r , redressed velocity signal; v_d , default velocity (30°/s); w , weight of v_r ; G_0 , gain factor; v_p , internal representation of platform velocity (“perceived velocity”); D_p , perceived displacement; D_d , desired displacement; Δ , detection threshold. *Lower panels* show fits of the model to experimental data $G_T=f(D_d, v_p)$ from conditions V and P (same data and same symbols as in Fig. 2 panels V and P); model parameters and goodness of fit (*GoF*, = variance explained by model/total variance) as listed in each panel. Note that the two (first series) or three (second series) curves in each plot have not been fitted separately for each velocity but en bloc

scheme that we have discussed above), the interaction of the vestibular and podokinesthetic cues in scenarios of this type still can be viewed as a particular way of sensory fusion. Moreover, the characteristics of the targeting gain indicate that conscious and unconscious cognitive mechanisms presumably are important and ever present elements of any fusion mechanism supporting naviga-

tion. These mechanisms draw on explicit and implicit situational information and on internal expectations, and compensate for much of the vestibular system’s imperfections during target-directed navigation.

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Appendix

Figure 6 (*upper part*) shows a translation, into a formal model, of our hypotheses regarding the extrapolation of the decaying vestibular signal and the intervention of cognitive factors during this process. The elements inside the *dashed outline* are those thought to constitute the blocks “Recover” and “Cognition” in Fig. 5. Note that the model is descriptive and not optimised in the statistical sense.

The model's first stage represents the peripheral vestibular system which senses angular platform velocity V . Because it is essentially a high-pass with time constant $\tau=5$ s, a decaying exponential will appear at its output (v) if V is a step function (as in the present experiments). To fill in for this fading signal, an integrator with gain $1/\tau$ operates in parallel to the direct pathway from the vestibular system; in Laplace notation this combination has transfer function $1+1/s\tau$, which is exactly the inverse of the vestibular high-pass. Because during long-lasting rotations (duration $>3\tau$) the integrator is charged to the full value of V which it then holds indefinitely (at least in theory) while the signal of the direct pathway vanishes, it can be considered an extrapolator. To insure stability in the case of $V=0$, the following stage features of a threshold element which fends off the drift that conceivably would arise in the extrapolating integrator (as in any real world integrator); we here assume a threshold value of $v_0=1.2^\circ/s$ (cf. Mergner et al. 2001). The velocity signal recovered in this way (v_r) is an almost ideal replica of the actual velocity V , except for the effect of the threshold. To account for our hypothesis that in the absence of a "real" (i.e. not reconstructed) vestibular signal also cognitive factors such as expectations based on the situational context and previous experience contribute to the targeting performance, the next stage calculates a weighted average of v_r and of a default velocity v_d , yielding $w \cdot v_r + R(1-w) \cdot v_d$; $R=1-\exp(-v_r^2)$ is a "regularising" function which insures that no default velocity signal arises if $v_r=0$ (otherwise G_T would reach infinitely large values), and which is close to unity for $v_r>2$. The weight factor w can be viewed as a measure of how much confidence is put into the reconstructed velocity v_r , while v_d represents Ss' expectation in the absence of all sensory information (we here assume $v_d=30^\circ/s$). Gain element G_0 ($G_0>1$) accounts for the global tendency towards overestimation (undershoot of target). The signal at the output of G_0 is an internal representation of platform velocity (v_p , "perceived velocity") given by

$$v_p = G_0 \cdot \{w \cdot (V - v_0) + R \cdot (1 - w) \cdot v_d\} \quad (2)$$

which for $V>v_0+2$ becomes

$$v_p = G_0 \{w \cdot (V - v_0) + (1 - w) \cdot v_d\}.$$

v_p is integrated to yield the currently perceived angular displacement (D_p) of the platform which, during passive rotation, equals perceived self-displacement in space. When D_p reaches the desired value D_d plus a fixed threshold Δ , Ss will signal fulfilment of their task. Therefore, the time (t) from start to the Ss' on-target signal can be obtained from

$$D_d + \Delta = D_p = v_p \cdot t$$

Moreover

$$D_a = V \cdot t$$

hence

$$G_T = D_a/D_d = V/v_p \cdot (1 + \Delta/D_d)$$

which is Eq. (1) referred to above in "Effect of turning velocity on vestibular targeting".

As pointed out in the Discussion, we hypothesise that the mechanism outlined above does not only concern the vestibular velocity signal but actually processes the difference between the vestibular and the transformed podokinesthetic signals, i.e. $v-p^T$ in terms of Fig. 5. During active turning this difference is zero. From Eq. (2) it is clear that no platform displacement will be signalled in this situation because then also the "regularising" function R becomes zero. Hence no platform displacement will be perceived, as postulated by the *eigenmodel* concept. On the other hand, during treadmill stepping, pod^T is the only constituent of $v-p^T$ and will give rise to exactly the same G_T curves as a pure *ves* signal would, except for the sign. To show how far this postulated similarity is borne out in reality, the *lower part* of Fig. 6 presents fits of the above model to the experimental data obtained in the V and P conditions, with w , G_0 and Δ as free parameters. As evident from these fits, within each of the two series, the weighting of stimulus velocity V was quite similar during conditions V and P (compare the values of parameter w). Because w determines by how much the G_T curves are vertically spaced for different values of V , this similarity supports our hypothesis that the velocity dependence of the vestibular and the podokinesthetic targeting gains is shaped by the same mechanism.

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