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RESEARCH ARTICLE

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Vestibular, optokinetic, and cognitive contribution to the guidance of passive self-rotation toward instructed targets

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Abstract We ask how vestibular and optokinetic information is combined ("fused") when human subjects who are being passively rotated while viewing a stationary optokinetic pattern try to tell when they have reached a previously instructed angular displacement ("targeting task"). Inevitably such a task entices subjects to also draw on cognitive mechanisms such as past experience and contextual expectations. Specifically, because we used rotations of constant angular velocity, we suspected that they would resort, consciously or unconsciously, to extrapolation strategies even though they had no explicit knowledge of this fact. To study these issues, we presented the following six conditions to subjects standing on a rotatable platform inside an optokinetic drum: V, pure vestibular (passive rotation in darkness); O, pure optokinetic (observer motionless, drum rotating); VO, combined (passive rotation while viewing stationary drum); Oe, optokinetic extrapolation (similar to O, but drum visible only during first 90° of rotation; thereafter subjects extrapolate the further course in their minds); VOe, combined extrapolation (similar to VO, but drum visible only during first 90°); AI, auditory imagination (rotation presented only metaphorically; observers imagine a drum rotation using the rising pitch of a tone as cue). In all conditions, angular velocities (v_C) of 15, 30, or 60°/s were used (randomized presentation), and observers were to indicate when angular displacement (of the self in space or relative to the drum) had reached the instructed magnitude ("desired displacement", D_D; range 90–900°). Performance was analyzed in terms of the targeting gain (G_T = physical displacement at time of subjects' indication / D_D) and variability ($\%E_R$ = percentage absolute deviation from a subject's mean gain). In all six conditions, the global mean of G_T (across v_C and D_D) was remarkably close to veracity, ranging from 0.95 (V) to 1.06 (O). A more detailed analysis of the gain revealed a trend of G_T to be larger with fast than with slow rotations, reflecting an underestimation of fast and an overestimation of slow rotation. This effect varied significantly between conditions: it was smallest in VO, had intermediate values with the monomodal conditions V and O, and also with VOe, and was largest in Oe and AI. Variability was similar for all velocities, but depended significantly on the condition: it was smallest in VO, of intermediate magnitude in O, VOe, Oe, and largest in V and AI. Additional experiments with conditions V, O, and VO in which subjects repetitively indicated displacement increments of 90°, up to a subjective displacement of 1080°, yielded similar results and suggest, in addition, that the displacement perceptions measured at the beginning and during later phases of the rotation are correlated. With respect to the displacement perception during optokinetic stimulation, they also show that the gain and its variability are similar whether subjects feel stationary and see a rotating pattern, or feel rotated and see a stationary pattern (circular vection). We conclude that the vestibular and optokinetic information guiding the subjects' navigation toward an instructed target is not fused by straightforward averaging. Rather the subjects' internal velocity representation (which ultimately determines G_T) appears to be a weighted average of (1) whatever sensory information is available and of (2) a cognitive default value reflecting the subjects' experiences and expectations. The less secure the sensory information (only one source as in V or O, additional degrading as in Oe or AI), the larger the weight of the default value. Vice versa, the better the information (e.g., two independent sources as in VO), the more the actual velocity and not the default value determines displacement perception. Moreover, we suggest that subjects intuitively proceeded from the notion of a constant velocity rotation, and therefore tended to carry on the perception built up during the beginning of a rotation or, in the case of vestibular navigation, to compensate for the decaying vestibular cue by means of an internal recovery mechanism.

Keywords Perception of angular displacement · Vestibular-optokinetic convergence · Sensory fusion ·

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Navigation · Path integration · Targeting · Vestibular system · Optokinetic stimulation · Circular vection · Motion extrapolation · Cognitive cues · Bottom-up information · Top-down information

Introduction

For orientation and navigation in space, humans predominantly refer to visual landmarks. Yet, they also exhibit considerable navigational skills when none are available. Navigation without landmarks is performed by integrating (in the mathematical sense) signals of allothetic and idiothetic origin (Mittelstaedt 2000) reporting either self-motion velocity or incremental displacements, a process often referred to as *path integration* or *dead reckoning*. Most important in this respect are optokinetic signals which provide allothetic information, vestibular signals (inertial idiothesis), and (in case of active movements) podokinesthetic ones; that is, a compound of foot, leg and hip proprioception and of efference copy signals (substratal idiothesis). Intuitively, it is obvious that this multisensory convergence enhances the reliability of orientation as compared to when only a single type of information was available. This intuitive notion is supported by experimental evidence showing, for example, that estimations of angular self-displacement are less variable when an observer actively turns about his own axis (stepping around) than when he is rotated passively (Bakker et al. 1999; Jürgens et al. 1999; Marlinsky 1999); note that in the former case the observer can draw on both his vestibular sense and on podokinesthetic information, whereas passive rotation only gives rise to vestibular signals. Complementing these observations, we recently have shown that estimations based on combined vestibular-podokinesthetic information are also less variable than those observed with podokinesthetic information alone (Becker et al. 2002).

Drawing on systems theory, Howard (1997) has suggested that the various information sources contributing to spatial orientation are fused by weighted averaging such that each sensory channel is given a weight inversely proportional to its variability. In this way, the variance of the resulting perception would be minimized ("maximum-likelihood estimation"). The same principle also has been invoked, and in part experimentally corroborated, for other multisensory situations such as the discrimination of object dimensions from vision and touch (Ernst and Banks 2002) or the accuracy of hand-pointing guided by vision and proprioception (van Beers et al. 1999).

However, applied to the perception of angular self-displacements, Howard's averaging hypothesis cannot fully account for the observed results. Although the reduced variability of estimations based on *combined* vestibular-podokinesthetic information would seem to support this notion, the signed error observed in the study of Becker et al. (2002) was not compatible with averaging, at least not without additional assumptions. Moreover, the notion that vestibular information be included in an average of the type envisioned by Howard may also raise a fundamental a priori objection: Physiological and psychophysical evidence indicates that the vestibular cue has high-pass properties, with most behavioral responses to vestibular stimulation being governed by a time constant (τ) of 15–20 s (Guedry 1974; Mergner et al. 1996; Young 1981). Thus, upon literal application of the averaging hypothesis, one would expect a substantial decrease of the turning perception during sustained passive rotation in a lighted environment because of the diminishing vestibular contribution. In reality, nothing the like happens: after 1 min of spinning on a turning chair, we still feel rotated about as fast as in the beginning.

One way to account for this observation is to assume that the optokinetic channel behaves as a low pass with frequency characteristics complementary to the vestibular ones, and that turning perception simply reflects the sum of the two cues rather than a weighted average. This view may be an approximately correct description of visual-vestibular interaction at the level of the vestibular nuclei (Robinson 1977), where, following the onset an optokinetic pattern rotation, the optokinetically driven activity of many neurons rises only slowly to its final level (Waespe and Henn 1977). However the optokinetic signals reaching perceptual levels allow for an almost immediate perception of the full velocity; hence, they are faster than compatible with this complementarity hypothesis. Other models therefore have the perception of self-turning during passive rotations in a stationary visual environment determined exclusively by the optokinetic channel, leaving to the vestibular cue the role of verifying that the current optokinetic signal truly results from self-turning rather than from a rotation of the environment (Mergner et al. 2000).

Although the latter model quite successfully explains a number of psychophysical observations, it fails to, and is not meant to, account for the possibility that also information reflecting an observer's knowledge, experience, and expectation might shape his performance. This possibility is suggested, for example, by vestibular targeting experiments. In fact, a human observer who is being slowly rotated in darkness and is requested to signal when he thinks he has been displaced by, say 300°, in most cases delivers his signal too early (Bakker et al. 1999; Jürgens et al. 1999). This result conflicts with the predictions derived from the high-pass character of the vestibular system according to which the observer should deliver his signal too late or even never, because his vestibular cue vanishes before he feels a displacement of 300°. The apparent conflict is resolved if one accepts the possibility that in many situations humans can either improve or replace the decaying vestibular cue by some form of extrapolation.

The present report attempts to investigate the presumed role of such cognitive processes, and specifically of extrapolation, for the perception of self-rotation during a navigation task (indicating when an instructed angular displacement has been reached). To demonstrate the intervention of extrapolation, one has to show that the perception evoked by an only briefly presented information is maintained for more or less extended periods of time following the removal of the information. The vestibular cue is not the best choice for such an experiment because its natural way of disappearance during rotations of constant velocity cannot be experimentally manipulated without evoking new perceptions. Instead, we consider the contribution of optokinetic information to turning perception which can easily be discontinued without entailing a sensation of deceleration.

Another question addressed in this paper concerns the way that vestibular and optokinetic information is fused during the task of achieving a desired angular displacement. Because, within certain limits which will be reported in the Results, vestibularly guided angular navigation exhibits little signs of a deficiency in the low-frequency range (be it as a result of extrapolation or for other reasons), the a priori objection against an inclusion of vestibular information into an averaging mechanism for sensory fusion mentioned above does not apply. We therefore pick up on the suggestion of Howard and ask two questions:

1. Can the targeting performance during passive rotation in a stationary visual environment without landmarks (combined vestibular-optokinetic stimulation) in any way be explained as an average of the performances resulting when either only vestibular or only optokinetic information is available?
2. Does the combination of vestibular and optokinetic information reduce the variability of targeting performance as compared to when only vestibular or only optokinetic information is available?

There exist a number of reports examining the interaction between vestibular and optokinetic signals in tasks probing the perception of angular self-displacement. However, many of them seek to identify mechanisms of interaction in the frequency domain (Zacharias and Young 1981) and are mostly based on sinusoidal stimulation (Mergner et al. 2000), or are specifically interested in the phenomenon of circular vection (for reviews, see Dichgans and Brandt 1978; Young 1981) and in the resolution of conflicts arising from discordant stimuli (Waespe et al. 1980; Probst et al. 1985). Experiments along the lines that are being pursued in the present paper have been conducted by Bles (1981) and by Bakker et al. (1999). From Bles' report it is difficult to extract enough data for a meaningful test of the averaging hypothesis. On the other hand, from the data published by Bakker and colleagues, one can deduce that the combination of vestibular and optokinetic information curtailed variability to some degree. Moreover, during combined stimulation, the signed error of targeting accuracy was intermediate to those obtained with either pure vestibular or pure optokinetic stimulation. Taken together, these observations would seem to support the averaging hypothesis. However, because these authors used a "virtual reality" display with a fairly small field of view to generate optokinetic stimuli, it is questionable whether their results also apply to rotations under more natural conditions. Significantly, their subjects judged the optokinetic condition more difficult than the vestibular one, whereas in our experience just the opposite is true if optokinetic stimulation is generated by means of an optokinetic drum. These considerations convinced us that it was appropriate to re-examine how vestibular and optokinetic information interact during angular navigation.

Methods

Subjects

Fifteen paid volunteers (mostly undergraduate students), aged 20–35 years (8 male, 7 female) served as subjects. All had normal (or corrected-to-normal) vision and were free of any known neurological pathology. 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. However, subjects were kept naive as to the *specific* goals of the experiment in order to prevent the formation of preconceptions that could affect their responses.

Equipment

Subjects stood at the center of a turning platform and were surrounded by an optokinetic drum (80 cm radius). The drum was lined with a Julesz pattern consisting of black and white squares subtending 0.5° which was divided into an upper and lower half by a horizontal white stripe at eye level (height 8°). The turning platform and the drum were driven by servo-motors under control of PC software; there were no noticeable vibrations or jolts during rotation. Subjects' head position was recorded by a potentiometer mounted overhead and coupled, by means of a lightweight, flexible yet torsionally rigid hose, to a helmet-like harness worn by the subjects. Integrated into the harness was a wireless headphone delivering a masking noise during rotations and serving for verbal communication. Head-to-trunk rotations were minimized by an orthopedic neck collar. For their responses, subjects had pushbuttons in both hands. All relevant signals were sampled at 1 kHz and stored on disk.

Procedures

Subjects were exposed to nine different experimental conditions to be performed on 3 different days. On the 1st day we assessed the basic characteristics of turning perception during vestibular, optokinetic, and combined stimulation as reflected by subjects' performance in a targeting task. On the 2nd day we explored how these characteristics change after the early removal of a sensory cue when subjects have to cope with impoverished sensory information. Finally, on the 3rd day, a subgroup of our subjects (12) were exposed to 3 conditions aimed at characterizing more thoroughly the temporal course of the turning perception. Each condition was run in a separate session lasting about 40 min; between sessions there were breaks of at least 10 min.

Targeting experiments (1st day)

Condition V. Pure vestibular. Subjects were passively rotated in complete darkness by means of the platform.

Condition O. Pure optokinetic. The platform was stationary and subjects stared at the illuminated optokinetic pattern rotating about them.

Condition VO. Combined vestibular *and* optokinetic. Subjects were passively rotated by means of the platform and viewed the optokinetic pattern, which remained stationary in space.

Trials. At the outset of each trial, the magnitude of the *desired displacement* (D_D) was announced (details below) and a warning tone (1000 Hz, 0.5 s) was sounded. Subjects then were presented with a platform or pattern rotation at one of three constant velocities (v_C=15°/s, 30°/s, or 60°/s); these rotations were reached by means of a brief initial acceleration epochs (raised cosine velocity profile lasting 0.5 s for 15°/s and 30°/s rotations, and 1 s for 60°/s). During rotation subjects were to continuously monitor their perception of angular displacement and to press the right button for two events: (1) when perceived displacement reached a value of 90°, and (2) when it reached the previously instructed target value D_D. Following the 2nd button press, the rotation was smoothly, though perceptibly, decelerated to a full stop and an end-of-trial tone (800 Hz, 0.2 s) was sounded. Subjects then were asked to score their confidence as to how accurately they had indicated the target angle in terms of German "school marks" (1–6; 1, absolutely confident; 6, absolutely unconfident).

Sessions. To familiarize subjects with the details of the different conditions, each session began with a short learning sequence of 4 sample trials during which subjects received feedback about their targeting performance. Thereafter the experiment proper was started, during which no feedback was given.

In each session the desired displacement D_D (i.e., the instructed target angle) had magnitudes of 150°, 210°, 270°, 360°, 450°, 540°, 720°, and 900°. In order to limit trial duration, the magnitude was confined to 450° for v_C=15°/s, and to 720° for 30°/s. Hence, there were 20 combinations of D_D and v_C in a session which each occurred once for each direction (left, right), resulting in a total of 40 trials per session. The order of presentation in a session was governed by one of three pseudorandom lists which varied among sessions and subjects in a balanced way. Also, the order of the 3 experimental conditions was randomized across subjects.

Instructions and read-out of perception. To read out subjects' perception of displacement, we asked subjects to signal the instant when, according to their perception, the desired angular displacement (D_D) had been reached (cf. above). D_D was announced, at the outset of each trial, in terms of full, half, or quarter turns, complemented by segments of ±30° where required (e.g., 210° was "half a turn plus 30°"). After learning the magnitude of D_D and before the rotation was started, subjects were to imagine their current position as a reference direction in space and to associate it with an imagined detail of the (invisible) experimental room (a door, a wall, or the like). During rotation they then were to continuously track in mind the growing angular displacement of the self in space (conditions V or VO), or of the displacement between the drum and the self (condition O). Their first button signal (completion of 90°) was solicited mainly to make procedures comparable with those used on the 2nd day, whereas the second signal (completion of desired displacement) was meant to mimic a perception-based decision during a natural targeting behavior.

To facilitate subjects' task and to homogenize their strategies, it was recommended that they mentally accumulate successive chunks of 90° perceptions. Depending on the experimental condition, different metaphors were suggested to subjects as means to evoke, in their minds, a picture of how the rotation proceeds. In conditions V and VO, they would conceive of their nose as a rotating pointer that sequentially aims at the various structures of the imagined room. In condition O they would mentally mark, at the outset of the trial, the pattern segment they just were facing and then would imagine during rotation when their shoulders were pointing to the marked area, then their rear, and so forth; however, they were strictly discouraged to try and identify details of the pattern such that an exact counting of full turns would become possible. During long-lasting optokinetic stimulation (O), most subjects would experience an illusory self-rotation in space (circular vection, CV); subjects were to signal such an event by pressing the left button, and to try to continue their mental accumulation of angular displacement, drawing now on the illusory self-rotation relative to the (apparently stationary) drum, instead of on their perception of drum rotation relative to the self. Finally, in all conditions it was stressed that subjects refrain from resorting to time estimations.

Targeting with extrapolation (2nd day)

Condition Oe. Optokinetic with extrapolation. Identical to O, except that drum illumination was switched off by subjects' 1st right button press, i.e., upon reaching a *subjective* displacement of 90°. Thereafter, subjects were to extrapolate the ongoing drum displacement solely by imagination and to indicate by the 2nd button press when they thought it had reached the desired value.

Condition VOe. Combined vestibular *and* optokinetic with extrapolation. Identical to VO, except that illumination was again switched off after reaching a subjective displacement of 90°. Because platform rotation continued, the vestibular signal remained identical to that in condition V.

Condition AI. Acoustically induced turning imagination. Subjects were first trained to associate optokinetic movements of 15, 30, or 60°/s with an acoustical cue consisting of a pure tone (delivered by headphone) with pitch increasing at a rate of one octave per 90° of angular drum displacement; thus, the rate of pitch increase was an indicator of turning velocity. During experiments proper, subjects stood motionless in complete darkness, listened to the tone, and tried to imagine the associated drum rotation. Much like in the other conditions, subjects were asked to signal (1st button press) when they thought that the (imagined) rotation had covered 90°; thereupon, the tone was silenced and subjects continued to mentally track the imagined rotation until they thought that it had accomplished the desired displacement (2nd button press). All other procedures and instructions were similar to those of the 1st day.

Repetitive displacement indications (3rd day)

Condition Vr90. Vestibular with repetitive 90° indications. Similar to V (passive rotation in darkness), except that subjects were to indicate each consecutive subjective displacement of 90° by pressing the right button upon passing 90°, 180°, 270°, and so forth, until reaching a final subjective displacement of 1080° (three full turns). There were 7 rotations at 15°/s, 6 at 30°/s, and 8 at 60°/s, which occurred in random order. Again, subjects were asked to concentrate on their perception of angular displacement and not to try and base their responses on time estimations. Subjects were to indicate verbally if, during the course of a rotation, their sensation of being rotated disappeared; in such a case rotation was stopped prematurely.

Condition Or90. Optokinetic with repetitive 90° indications. Identical to Vr90, except that the stimulation was optokinetic as during O, with subjects indicating successive 90° chunks of relative displacement between the pattern and the self. Subjects were instructed to press the left signal button should they begin to experience circular vection; thereafter they were to continue with the right button, signaling now consecutive 90° epochs of (apparent) self-rotation in space.

Condition VOr90. Combined vestibular *and* optokinetic with repetitive 90° indications. This was identical to Vr90, except that subjects viewed the (stationary) optokinetic pattern during rotation.

The order of presentation of these conditions was again randomized across subjects.

Data analysis

Unless explicitly stated otherwise, all statistical tests were carried out in the form of repeated-measures, 2- or 3-way ANOVAs followed by post hoc tests (Tukey HSD) using a commercial package (Statistica). These tests were restricted to the range 150°≤D_D≤450° covering those five values of the desired displacement which occurred with each of the three turning velocities. Effects and differences will be called significant if $P<0.05$ and highly significant if $P<0.01$. Details of other procedures will be reported in the respective contexts of the description of results.

Results

Targeting experiments

The analysis of the data obtained during the six targeting experiments of the first 2 days will be centered on the relationship between the "achieved" displacement (D_A) and the desired displacement (D_D), where D_A represents the physical displacement of the platform, or of the drum, recorded at the instant of the 2nd button press. Because subjects were supposed to deliver this signal upon *perceptually reaching* the instructed target value of D_D, we will interchangeably use the terms *desired displacement*, *target,* and *perceptually reached displacement* in the following, whichever fits better into the context.

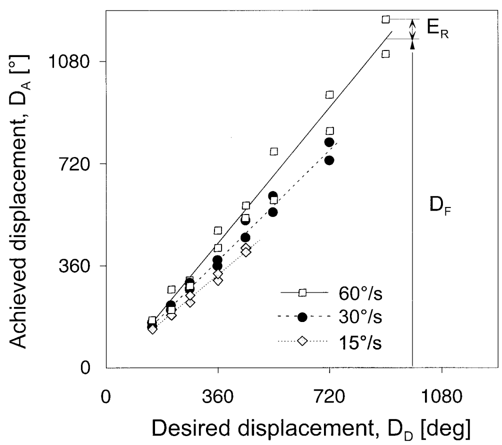

Fig. 1 Scatter plot of achieved displacement (D_A) versus desired displacement (D_D). Data from one subject, condition O. Note separate linear fits for the three velocities of drum rotation. E_R, random error defined by $|D_F - D_A|$, where D_F represents the value predicted by the linear regression of D_A on D_D

Gain

In the vast majority of the cases, the achieved displacement was an approximately linear function of D_D as illustrated in Fig. 1 for a sample subject in condition O. The subject shown in Fig. 1 is typical for the whole group of subjects in that the slope of this function depended on the velocity (v_C) of drum rotation. Indeed, during 60°/s rotations, the subject pressed the response button too late so that the achieved displacements became larger than the desired target values (slope of regression of D_A vs D_D exceeds unity); on the other hand, with 30°/s rotations, D_A almost equaled the desired value (slope≈1), and at 15°/s it became too small (slope<1). Note that the overshoot of D_A during fast rotations suggests that the subject *under*estimated the drum's actual displacement and, vice versa, that the undershoot during slow rotations is indicative of an *over*estimation.

The velocity-related differences suggested by Fig. 1 are best appreciated if the subjects' performance is expressed in terms of the *targeting gain*, defined by $G_T=D_A/D_D$. Figure 2 gives a synopsis of the population averages of G_T calculated for all six conditions considered here, represented as functions of the desired displacement. Panel O confirms that the velocity dependence exhibited by the sample subject of Fig. 1 is a phenomenon representative of the population as a whole; it is here reflected by the vertical separation of the G_T curves according to stimulus velocity. Like the sample subject, the population as a whole underestimated fast rotations (button pressed too late, $G_T>1$; continuous curves), was

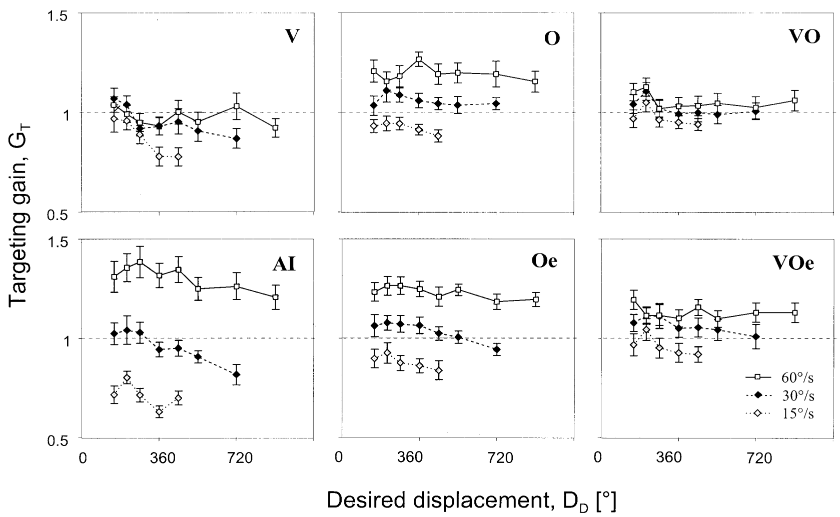

Fig. 2 Targeting gain (G_T) as a function of desired displacement (D_D) in the 6 targeting conditions; G_T was averaged separately for each of the three turning velocities (15, 30, 60°/s; *dotted, dashed, solid lines*); *N*=15 subjects. *Error bars* ±1 SE

Table 1 Targeting experiments: ANOVA of the effects of experimental condition (*cond*), turning velocity (v_C), and magnitude of desired displacements (D_D)

Effect	*df*	*F* level	*P* level
cond	5	2.39	0.046345
v_C	2	90.40	0.000000
D_D	4	4.25	0.004466
cond×v_C	10	25.48	0.000000
cond×D_D	20	1.98	0.008554
v_C×D_D	8	3.30	0.001997
cond×v_C×D_D	40	0.96	0.546329

Table 2 Targeting experiments: mean velocity spread index (*VSI*), random error ($\%E_R$), and rating of confidence into own performance by means of school marks (*SM*; smallest score corresponds to highest confidence). Note that SM is tightly correlated with both VSI (r=0.88) and %Er (r=0.91)

Condition	VSI	$\%E_R$	SM
V	6.0	12.21	3.33
O	10.3	9.85	3.18
VO	3.4	9.18	2.95
Oe	14.8	10.68	3.26
VOe	7.4	9.98	3.05
AI	30.9	12.61	3.68

about veridical during rotations at intermediate velocities (GT≈1, dashed), and overestimated slow rotations (G_T<1; dotted).

With regard to the dependence of the targeting gain on the experimental conditions, Fig. 2 suggests that three aspects have to be considered: (1) the global magnitude of G_T, that is, its average taken over all values of v_C and D_D; (2) its dependence on turning velocity as reflected by the vertical separation of the curves, and (3) the way G_T varies as a function of D_D. Accordingly, a 3-way ANOVA of G_T was run with factors *experimental condition, velocity,* and *desired displacement*. As shown in Table 1, all main effects and all 1st-order interactions were significant or highly significant. Post hoc comparisons indicate that:

1. The global magnitude of G_T was similar and remarkably accurate in all conditions (ranging from 1.02 to 1.06), except for V where it reached only a value of 0.94; this 10% difference was only close to significance though
2. The mean of G_T across conditions and velocities was a weakly decreasing function of D_D; however, most differences between small and large displacements are significant in condition V only (hence the highly significant *condition* × D_D interaction evident from Table 1).
3. In all conditions, G_T was larger during fast rotations than during slow ones. However, the extent to which the angular velocity modulated G_T varied considerably among conditions (note the highly significant *condition* × v_C interaction in Table 1). While during conditions O, Oe, and AI both of the inequalities $G_T(60)>G_T(30)>G_T(15)$ were significant, only one was during V and VOe, and none during the combination VO.

To analyze in more detail the dependence of G_T on turning velocity, a "velocity spread index" (VSI) was calculated based on the following considerations: If subjects translated the desired displacement magnitude into a temporal cue using a fixed proportionality irrespective of the actual magnitude of the turning velocity, G_T would vary by a ratio of 60/15=4; we assigned this case a VSI of 100%. If, on the other hand, subjects' estimates took the turning velocity perfectly into account, G_T would be completely independent of v_C; we wished this case to be reflected by a VSI of 0%. Hence:

$$\mathrm{VSI} = 100\% \cdot [\mathrm{G_T}(60°/\mathrm{s})/\mathrm{G_T}(15°/\mathrm{s}) - 1]/3 \qquad (1)$$

The means of VSI across subjects and across those five values of D_D that occurred with every stimulus velocity are presented in Table 2 (1st column). VSI was smallest in condition VO (3.4%) and largest in AI (30.9%), increasing in the order VO<V<VOe<O<Oe<AI. A two-way ANOVA with factors *condition* and *desired displacement* confirmed the highly significant effect of the experimental condition. According to post hoc comparisons, the following inequalities were significant: VO<(VOe, O, Oe, AI); (V, VOe)<(Oe, AI); (O, Oe)<AI.

Referring to Fig. 2, we complement these quantitative data by a number of qualitative observations: First, note that all effects revealed by ANOVA also appear to hold for those values of D_D which could not be included in the ANOVA ($D_D \geq 540°$). In particular, vestibular targeting continued to be either correct or to undershoot even when large displacements were requested, contrary to what would occur if perception were determined by a central vestibular time constant of 15–20 s, as often presumed. Moreover, the separation of the gain curves according to velocity (comparing now only 30°/s and 60°/s) continued to exhibit the same rank order across conditions (VO smallest, AI largest). It is of particular interest that also in conditions VO and VOe the separation remained smaller than during O and Oe, respectively. Thus, there is no sign that the vestibular contribution would vanish during large and, hence, long displacements, since, otherwise, these separations would tend to approach the magnitudes characteristic for O and Oe.

It is also interesting to compare the conditions in which subjects were forced to extrapolate, because some (VOe) or all (Oe) afferent information had been removed soon after the beginning of the trials, to those where the optokinetic cue was permanently available (VO and O, respectively). Impoverishing the available afferent information in this way changed targeting performance remarkably little, except for the increase in VSI reported above (significant for VOe vs VO, *n*.s. for Oe vs O).

An increase in the velocity dependence to a still greater extent also was the main result of further impoverishing the available afferent information in con-

Table 3 Targeting experiments: correlation between targeting gain (G_T) and gain calculated from subjects' first 90°-indications (G_{90}), mean from 15 subjects. Left, coefficient of correlation; right, relative frequency of significant (P<0.05) correlation in individual subjects. Column *all v*, grand means across velocities

Condition	Coefficient of correlation				Frequency of significant correlations			
	15°/s	30°/s	60°/s	All *v*	15°/s	30°/s	60°/s	All *v*
V	0.64	0.56	0.49	0.56	0.60	0.67	0.73	0.67
O	0.59	0.37	0.47	0.48	0.60	0.47	0.47	0.51
VO	0.54	0.50	0.45	0.50	0.60	0.67	0.53	0.60
Oe	0.57	0.42	0.45	0.48	0.73	0.33	0.40	0.49
VOe	0.53	0.30	0.36	0.40	0.60	0.20	0.40	0.40
AI	0.46	0.48	0.31	0.42	0.47	0.53	0.40	0.47

dition AI where, in addition to be temporally limited, information was presented only metaphorically (pitch increase in auditory cue); yet, apart from the increase in VSI, the pattern of G_T-curves obtained with AI was fairly similar to those found during Oe, with performance during intermediate velocities (30°/s) being close to veridical.

Taken together, the results from conditions Oe, VOe, and AI suggest that navigation may be helped by cognitive mechanisms. Specifically, it is tempting to speculate that one such mechanism may be the ability to store perceptions acquired early in the course of a movement so that they can be substituted for sensory information which either gradually fades away (as in condition V) or is suddenly removed (as in Oe). If this idea is true, one would expect that when subjects overestimate the initial part of a rotation (and therefore press the signal knob for the first 90° displacement too early), they will continue to overestimate and, therefore, fall short of the desired displacement. To test this possibility, the correlation between the subjects' gain at 90° (G_{90}) and their targeting gain (G_T) gain was determined. Specifically, for each subject we calculated the coefficients of correlation between G_T and G_{90} separately according to condition and velocity; the values of individual coefficients therefore are based on the 10, 14, or 16 trials of, respectively, 15°/s, 30°/s, or 60°/s turning velocity that occurred during each condition. About 50% of the thus-calculated coefficients of correlation were significant (lower margin of 95% confidence range exceeding zero). A 2-way ANOVA (factors condition and velocity) revealed a significant effect of turning velocity in our population of 15 subjects, and post hoc comparison indicated that the coefficients of correlation were significantly larger with rotations of 15°/s than with 30°/s or 60°/s (see Table 3).

Variability

In order to quantify the intrasubject variability of targeting performance, we considered the *random error* (E_R) which represents the subjects' deviation, during single trials, from their average performance, defined by $D_F=D_0+b\cdot D_D$, the linear fit of D_A vs D_D (cf. regression lines in Fig. 1); accordingly:

$$E_R = |D_F - D_A| \quad (2)$$

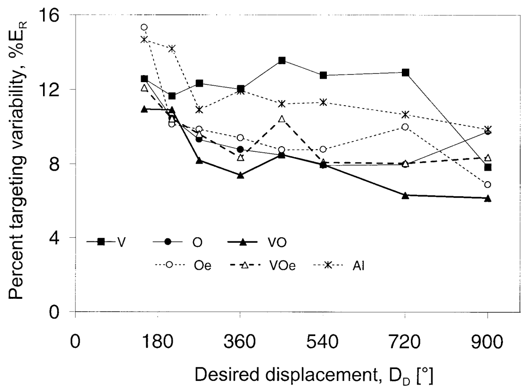

Fig. 3 Percentage variability ($100\%\cdot E_R$ / D_F; for definition see Eq. 2 and Fig. 1) of achieved displacement as a function of desired displacement, mean of 15 subjects. Data corresponding to the different turning velocities have been pooled (hence, up to D_D=450° the curves represent the mean from all three velocities, whereas for D_D>450 only trials of 30°/s and 60°/s could contribute, and for D_D>720 only trials of 60°/s). Experimental conditions as explained in legend (see text for acronyms). *Solid lines* and *filled symbols*, "normal" targeting experiments (conditions V, O, VO); *broken lines* and *open symbols*, experiments requiring extrapolation and/or imagination (Oe, VOe, AI). *Heavy curves* outline bimodal conditions (VO, VOe)

Because E_R increased in a roughly linear way with D_D in most cases, it was converted into a percentage value according to:

$$\%E_R = 100\% \cdot E_R / D_F \quad (3)$$

A 3-way ANOVA indicated highly significant effects on the percentage random error of both the experimental condition and the desired displacement, whereas the effect of turning velocity just failed to reach significance (P=0.0504) and mainly reflects a particularly large variability that occurred for a single combination of the factors displacement and velocity (150°, 60°/s; hence a highly significant $v_C \times D_D$ interaction). In Fig. 3, which plots $\%E_R$ as a function of the desired displacement, data therefore were pooled across velocities; the figure suggests that: (1) $\%E_R$ decreased as a function of D_D (mainly so in the range 150–360° where post hoc testing indicated a significant reduction), and (2) $\%E_R$ was smallest in the combined stimulus condition VO, whereas conditions V and AI exhibited the largest variability.

The minimum of VO had been expected, because in this condition subjects disposed of a maximum of sensory information. Accordingly, planned comparisons (linear contrast) with the other five conditions were conducted; these confirmed the variability during VO to be significantly smaller than during V and AI but failed to detect significant differences with respect to the remaining three conditions. Moreover, to test our hypothesis that the initial percept of self-rotation might govern much of the later targeting even if the available sensory information deteriorates in the course of a rotation, we also carried out a planned comparison between V and VOe, which suggested a significant reduction of $\%E_R$ in the latter condition. Thus, although VOe trials were for most of the time identical to V, subjects' performance exhibited less variability owing to the brief presence of an optokinetic stimulus at the beginning of these trials.

Occurrence of circular vection

In condition O most subjects experienced a circular vection (CV) in at least some of the trials. As described in Methods, they used a separate signal button to indicate when they entered this state of perception. Individual percentage frequencies of CV occurrence ranged from 0% to 97.5% of the trials. Not surprisingly, because the probability to develop CV increases with stimulus duration, the population average of this frequency was a rising, almost linear, function of the desired displacement (17% for desired displacements of 150°, 70% for 900°). CV latency was consistently shorter during fast as compared to slow rotations. It averaged about 8 s; because in trials of short duration only CV of short latency is observable, this value was determined from trials of long duration (large desired displacements).

Repetitive displacement indications

The experiments of the 3rd day (conducted with a subpopulation of 12 subjects) in which subjects repetitively indicated the completion of consecutive displacements of 90° were intended as control experiments to examine the following issues:

1. Do subjects in condition V really continue to perceive changes of angular position for as long as 30 s (e.g., when D_D=450°, v_C=15°/s) as their targeting gain suggests, in spite of the undeniable decay of the peripheral vestibular signal?
2. Does perceived angular position in fact increase at constant rate during each single trial, with the rate being already established after the first 90° of subjective rotation, as the correlation between G_T and G_{90} suggests?
3. Does the occurrence of circular vection during optokinetic stimulation (and the concomitant change from a perception of pattern motion to one of self-motion in space) lead to quantitative changes of subjects' indications—in other words, are these two visually mediated perceptions similarly calibrated with regard to the relative rotation between the pattern and the observer so that they can be used interchangeably?

Persistence of vestibular perception

Figure 4A provides a synopsis of the performance of the 12 subjects during the most demanding case of vestibular navigation, that is, during rotation at 15°/s. The figure plots the angular positions achieved (D_A, ordinate) at the time of subjects' button presses as a function of the desired displacement (D_D). Note that by "desired dis-

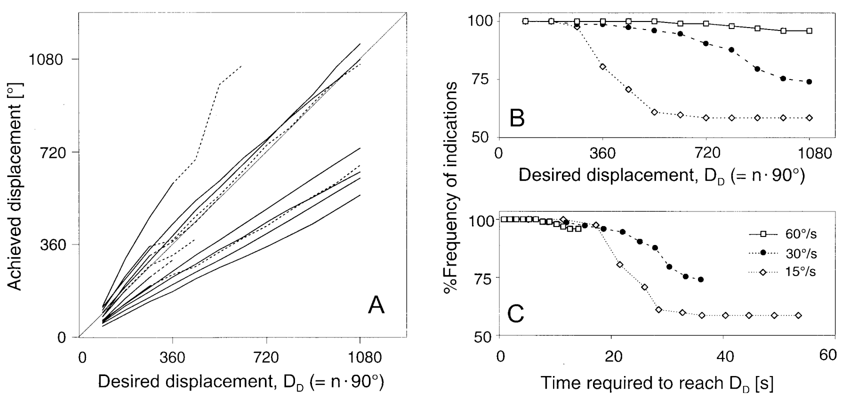

Fig. 4A–C Repetitive displacement indications, condition Vr90. **A** Achieved displacement (physical displacement by the time of the n^{th} 90° signal, n= 1, 2, ...12) during slow rotations (15°/s), plotted as a function of the desired displacement D_D (cumulated value of the increments which subjects were supposed to indicate, i.e., $D_D=n\cdot 90°$). Each curve represents the mean (N=7) of one subject; *dashed segments* indicate cases where N<7 because the subject's perception dropped out in some trials before perceptually reaching the corresponding displacements; curves terminate after the maximum displacement which the subject perceived in at least one of the trials. **B** Percentage frequency of subjects' indicating their reaching the desired displacements. Values of less than 100% indicate that some subjects no longer experienced a turning sensation in some or all of the trials, and therefore could indicate no more 90° increments of self-displacement. **C** Data of **B** replotted as functions of the time required to reach D_D

placement” we here no longer understand the single target value per trial that subjects indicated in the targeting experiments, but each of the consecutive 12 displacement values per trial (of magnitude $n{\cdot}90°$, n=1, 2, ..., 12) which subjects were supposed to indicate by delivering their n^{th} 90° signal; it could as well be described as the *perceptually reached displacement* inferred from the occurrence of the n^{th} signal. Each curve represents the mean of one subject. Dashed curve segments mark cases in which the subjects lost the sensation of self-turning in some trials before they perceptually reached the corresponding displacement; for example, in some of his trials the subject with the steepest curve in Fig. 4A experienced only four 90° increments (equivalent to a perceptual displacement of 360°) before he quit. Similarly, curves that do not continue beyond a desired displacement of $n{\cdot}90°$ represent cases where in *all* trials subjects lost their feeling of being turned before perceptually reaching a displacement of $(n+1){\cdot}90°$; for example, the subject just considered never experienced displacements larger than 630°. Interestingly, preceding the loss of vestibular turning perception, there was no accelerated rise of the curves and therefore no hint at a *gradual* decrease in perceived turning velocity as a precursor of this loss. Note that all subjects experienced displacements of up to 450° in at least some of their trials. Thus, by limiting D_D to 450° during 15°/s rotations in the targeting experiments, we adventitiously had chosen the maximum value up to which *all* subjects could entertain a vestibular perception of self-turning.

With faster turning, the sensation of self-rotation was less likely to disappear. This is illustrated in Fig. 4B which plots the mean percentage frequency at which subjects perceived, and hence indicated, their reaching the desired displacement. Whereas during slow rotation (15°/s) the early dropout of some of our subjects evident from Fig. 4A caused a fall of this frequency to a level of about 60% for desired displacements exceeding 540°, upon fast rotation (60°/s) all subjects would perceptually reach the maximum desired value of 1080° in almost every trial. When the frequency data of Fig. 4B are replotted as functions of the time required to reach D_D, the resulting curves collapse in a time range of about 0 – 18 s (Fig. 4C); within this time span, all subjects felt rotated during nearly all trials (drop-out rate <5%). After about 30 s, the subjects tending to drop out early had quit completely, while the other ones upheld a whole-body turning sensation in most of their trials for up to 53 s (mean time required to perceptually reach the maximum desired displacement of 1080°).

Rate of increase in perceived displacement

To demonstrate the evolution of our subjects’ perception during a trial, we have calculated the *instantaneous gain*, G_I, defined by $G_I=\Delta D_A/90°$, where ΔD_A represents the physical displacement that occurred between the $(n-1)^{th}$ and the n^{th} signal of the subjects. Fig. 5 (panels Vr90, Or90, VOr90) plots the mean of G_I as a function of $n{\cdot}90°$ (desired displacement); included in these averages are only those 8 of our 12 subjects who continued to have a vestibular perception up to 1080° during most of their trials. Note that, in contrast to Fig. 2, which for any given value of D_D shows the *mean* gain across the whole course of just those trials which were aimed to achieve this displacement value, in Fig. 5 each trial of appropriate velocity contributed to the G_I-curves with each of its n ($n\leq 12$) 90° indications. To the extent that subjects conformed to the experimental instructions, at the instants of the 90° signals their perception of self-displacement equaled the desired displacement; therefore the plots render the inverse of the rate at which their displacement perception increased. For example, during slow rotations in condition Vr90, the instantaneous gain stabilized at a level of about 0.72 after a perceptual displacement of 540° had been reached; this reflects a perceptual gain of 1/0.72=1.38.

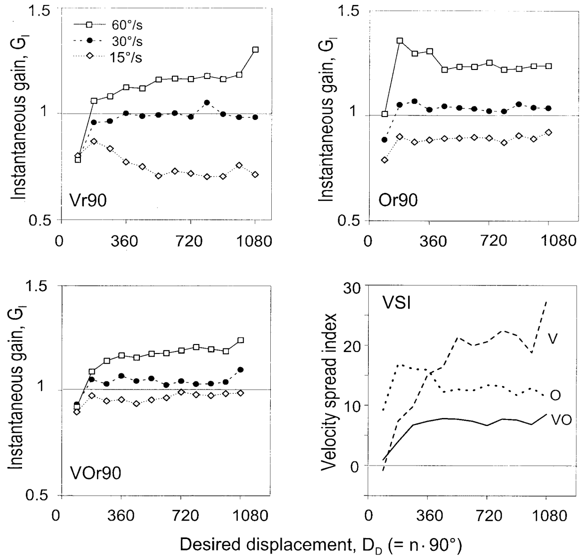

Fig. 5 Repetitive displacement indications. Panel s *Vr90, Or90,* and *VOr90*, instantaneous gain (G_I) as a function of the desired displacement ($n{\cdot}90°$). G_I is defined as $[D_A(n)-D_A(n-1)]/90°$, where $D_A(n)$-$D_A(n-1)$ represents the increment in physical displacement between successive 90° indications. *Horizontal line*, ideal gain (G_I=1, perceived displacement increment equals physical increment). The three experimental conditions are identified by their acronyms; turning velocities are discriminated by different symbols (see legend in panel *Vr90*). Panel *VSI*, velocity spread index calculated from the data in panels *Vr90, Or90,* and *VOr90*, using Eq. 1

Like the targeting gain in experiments V, O, and VO, G_I increased with turning velocity. The resulting velocity spread (Fig. 5, panel VSI) was again smallest in the combined condition (VOr90) and largest during optokinetic stimulation (Or90), at least if the same range of desired displacements is considered as in the targeting conditions ($D_D\leq 450°$). However, for $D_D\geq 450°$ the spread became largest in the vestibular condition (Vr90), where it reached the same order of magnitude as in condition AI of the targeting experiments.

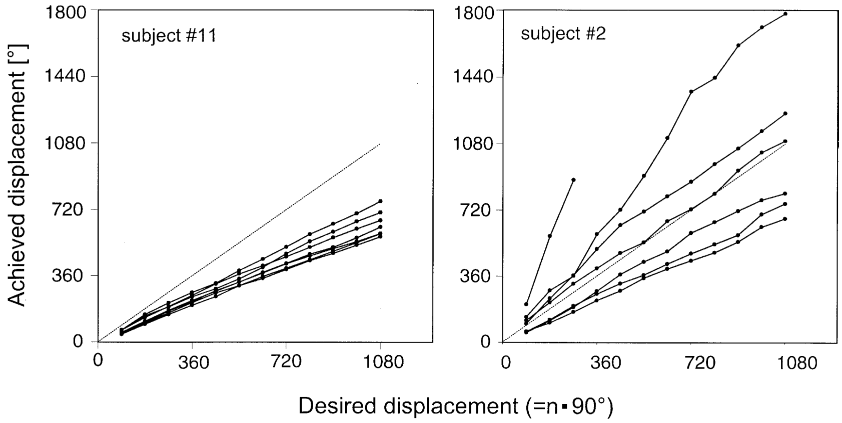

Fig. 6 Repetitive displacement indications, vestibular condition (Vr90). Examples of displacement indications from two subjects during slow rotations (15°/s) marking extremes of intraindividual variability (small in *11*, large in *2*)

To further pursue the hypothesis that the perception established during the initial phase of a trial might determine what is perceived in the later course of that trial, we have inspected the increase in achieved displacement in individual trials. Figure 6 shows the individual trials of two subjects during rotations at 15°/s in condition Vr90 which represent extremes in terms intrasubject variability. Whereas in subject 11 the rate at which achieved displacement increased during his successive 90° indications was remarkably similar in his seven trials, it exhibited large trial-to-trial variations in subject 2. Remarkably, however, the curves of the latter subject form a bundle of diverging, more-or-less straight lines, with virtually no cases of cross-over, suggesting that if displacement perception is large during the initial phase of a trial it will be so also in the further course of this trial (curves with small slope in Fig. 6), and similarly if perception initially is small it will be small also later on (steep curves). For a quantitative corroboration of these observations, we calculated for each subject and condition $dG_I(D_D)$, the deviations of the instantaneous gain $G_I(D_D)$ during single trials from its mean value. We then pooled the deviations from all subjects and considered the coefficients of correlation between $dG_I(90°)$ and the values of dG_I for D_D=360°, 720°, and 1080°, respectively. As evident from Table 4, during vestibular stimulation (Vr90), all correlation values were positive and significantly different from zero; thus, the instantaneous gain during the whole course of a trial was positively correlated with the gain of the first 90° indication at the beginning of the trial. In the optokinetic condition (Or90), such a correlation existed only during slow rotations, and essentially no correlation was observed in the combined condition VOr90.

The lack of or smaller number of cases with significant correlation in conditions Or90 and VOr90 may be related to the fact that the range over which the instantaneous gain varied in single trials was smaller in these conditions than in the vestibular condition. Indeed, using the standard deviation of G_I as a measure of variability, a 3-way ANOVA suggested a significant effect of the factor condition, whereas turning velocity and desired displacement (which here is a measure of whether an indication was delivered early or late during a trial) had no effect. Post hoc analysis indicated that the standard deviation was significantly smaller during both VOr90 (SD 0.15; mean from all velocities and displacement values) and Or90 (0.17) than it was during Vr90 (0.25).

Table 4 Repetitive 90° indications: coefficients of correlation between instantaneous gain (G_I) of first 90° indication and G_I of 4^{th}, 8^{th}, and 12^{th} indication (i.e., after perceptual displacements ofD_D=360°, 720°, and 1080°, respectively) calculated from pooled data of all subjects. Column *all v*, mean of coefficients of correlation across all angular velocities; rows*all* D_D, mean of coefficients of correlation across the values calculated for D_D= 360°, 720° and 1080°

Cond	D_D	Angular velocity			
		15°/s	30°/s	60°/s	All *v*
Vr90	360°	0.46*	0.73*	0.32*	0.50
	720°	0.41*	0.61*	0.32*	0.45
	1080°	0.37*	0.50*	0.29*	0.39
	All D_D	0.41	0.61	0.31	
Or90	360°	0.48*	0.12	0.17	0.26
	720°	0.39*	–0.01	–0.11	0.09
	1080°	0.30*	0.36*	–0.26	0.13
	All D_D	0.39	0.16	–0.07	
VOr90	360°	0.16	0.08	0.01	0.08
	720°	0.12	0.05	0.13	0.10
	1080°	0.21*	0.13	0.22*	0.19
	All D_D	0.16	0.09	0.12	

* Significant positive coefficients

Role of circular vection

In our targeting experiment, a methodological problem occurred during prolonged optokinetic stimulation (condition O): as described above, after some variable latency most subjects would no longer perceive a rotation of the pattern relative to the stationary self, but feel rotated themselves (circular vection, CV). In that event, subjects had been told to add the now accumulating perception of self-displacement in space to the previously recorded pattern-to-self displacement (see Methods). However, this way of combining qualitatively different perceptions

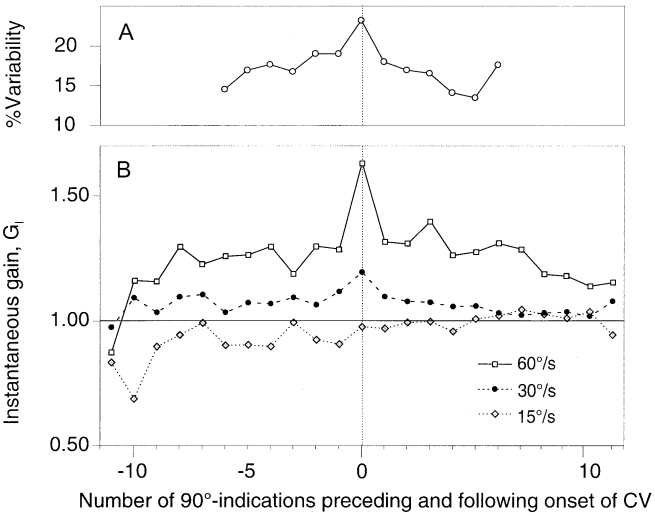

Fig. 7A, B Repetitive displacement indication, condition Or90. Percent intraindividual variability (percentage standard deviation; **A**) and instantaneous gain (G_I; **B**) before and after onset of circular vection (*CV*). Population averages of trials aligned with onset of CV. Abscissa value zero identifies the gain calculated for the interval between the last 90° indication without CV and the first indication after CV onset. Note that the number of averaged values declines in both directions along the abscissa because the original trials span only 12 indications. Because the same also holds for the number of available samples in each individual, the percentage variability curve is shown only for ±8 indications

makes sense only if these perceptions are based on the same calibration of the optokinetic flow. To test this assumption, we had the subjects signal the occurrence of CV also in the Or90 condition so that we could test whether the instantaneous gain prior to the onset CV was different from that after the onset. On average, CV began after 19.0 s, 15.7 s, and 8.5 s during rotations of 15°/s, 30°/s, and 60°/s, respectively. These values correspond to physical pattern rotations (achieved displacements) of 285°, 471°, and 512° and to perceptual displacements of 363°, 477°, and 435°. To compare the instantaneous gain before and after the occurrence of CV, we aligned the trials on CV onset by plotting G_I as a function of the number of 90° indications delivered before (negative abscissa values) and after (positive) CV onset. Fig. 7B shows the population average across the thus aligned trials. During rotations of 60°/s the first 90° indication following the onset of CV (abscissa value 0) was markedly delayed in comparison with earlier and later ones, resulting in a transient increase of the instantaneous gain, whereas no or only a very faint increase can be seen for 15°/s and 30°/s. Most importantly, however, there were no systematic gain differences between the indications delivered before and after CV had started, suggesting that, from a quantitative point of view, it is legal to pool data obtained during the two perceptual states that typically succeeded in condition O. This conclusion is also corroborated by the similarly constructed curve of percentage variability of G_I in Fig. 7A which is based on the mean, across subjects and velocities, of the intraindividual standard deviations of G_I. Like the gain, variability did show no significant changes after the onset of CV (except again for the interval during which this change occurred).

Scores of subjective difficulty and of confidence in own performance

At the end of the three targeting conditions tested on day 1 (V, O, VO) and day 2 (Oe, VOe, AI), subjects had been asked to rank the subjective difficulty of each day's conditions. On average, VO was felt to be the easiest paradigm of the 1st day (mean ranking 1.33; 11 of 15 subjects quoting "1"), followed by V (2.27) and O (2.40). On the 2nd day, VOe (1.50) was rated slightly easier than Oe (1.71), whereas AI (2.79) was rated most difficult by 13 of the 15 subjects.

Also, after each trial subjects rated their self-confidence into how well they had achieved the desired displacement. On a single-trial basis, the confidence scores (school marks) were completely uncorrelated with the accuracy of targeting both in terms of the targeting gain (G_T) and the deviation from the individual subjects' fit (E_R). Thus, there were trials where subjects grossly missed the target and yet were highly confident of their performance, whereas on other trials they would perfectly achieve the desired displacement but feel completely lost. Yet, on average, the scores were highly dependent on the experimental condition (ascertained by ANOVA). Subjects were most confident in condition VO and least confident in AI, with the other conditions ranging in between in almost the same order as observed with the percentage random error (Table 2). In conditions V and VOe, confidence depended strongly on turning velocity, with subjects feeling increasingly more secure as angular velocity was raised, a relationship that did not hold for the other conditions (hence a highly significant interaction *experimental condition* × *velocity*).

Discussion

Conditions V, O, and VO of the present experiments examined the contribution of optokinetic information to the perception of angular self-displacement in a targeting situation and compared it with that of vestibular information which we have characterized already in a previous study using very similar conditions (Becker et al. 2002). In particular, we were interested to see whether and how the combination of these two types of information would improve perception over that observed with either information alone; by "improve" we here understand a reduction of the signed error (gain closer to unity) or of the random error, or both.

Optokinetic contribution

Somewhat surprisingly, a previous report by Bakker et al. (1999) on this topic had suggested that displacement perception based on optic flow is in no way better (in terms of veracity, intraindividual variability, and subjective confidence) than a perception drawing on vestibular information; actually, these authors found it even to be slightly worse. Also, according to the same authors, the *combination* of vestibular and optokinetic information does not improve veracity over what is observed if only vestibular information is available, but apparently causes errors intermediate to those obtained with either of the two monomodal stimulations. On the other hand, the combination reduced intraindividual variability by a factor of about 1.26 (as calculated from Table 1 of Bakker et al.). Taken together, these results would suggest that perception is based on an average of vestibular and optokinetic information.

Our findings differ from those of Bakker et al. in a number of respects: in the optokinetic condition (O) mean targeting gain (G_T) was significantly larger than in the vestibular condition (V) and reached values almost twice as large as reported by Bakker; targeting variability was lower; and subjective confidence was better (although not to a significant level). Similar observations also hold for the comparison between our conditions Or90 and Vr90. Most importantly, however, the gain obtained when vestibular and optokinetic information were combined (VO) cannot be interpreted as an average of the gains observed with V and O, respectively. To appreciate this fact, consider the top panels in Fig. 2: averaging the G_T curves of panels V and O separately according to turning velocity cannot yield a set of curves as in panel VO, where velocity spread is smaller than in both V and O. Indeed, the set of curves averaged from V and O exhibits a mean velocity spread of 7.8% as compared to 3.4% for VO, a difference which is highly significant [2-way ANOVA with factors condition = {VO, average(V,O)} and desired displacement]. Note that this difference would be even larger (VSI 8.6%) if, according to the rule proposed by Howard (1997), G_T(O) was weighted more heavily in the average than G_T(V) because it has less variability. The same arguments also apply to the results of the repetitive indications experiments, where the curves of instantaneous gain (G_I) obtained with VOr90 cannot be averages of those found for Vr90 and Or90, respectively.

Noticeably however, if the above comparison between VO and average(V,O) was carried out *without* distinguishing between turning velocities (pooling the data from all velocities), the average of V and O would become virtually identical to the results of the combined stimulation. Combined with the observation of minimal variability during VO, such a failure to discriminate velocities could lead to the erroneous conclusion that optokinetic and vestibular information is fused by straightforward averaging. Below we will argue that the same holds true for experiments in which rotations occur at a single velocity only, or at velocities that vary over a small range only. If this point is taken into account, the results of Bakker et al. (1999) can be considered compatible with the present ones as far as the perception during combined stimulation is concerned. On the other hand, the small gain, the large variability, and the low confidence of their subjects during optokinetic stimulation are most likely consequences of the use of a "virtual reality" display which does not cause a stimulation as potent as a rotating *real* optokinetic drum. For the same reason, the subjects of Bakker et al. apparently never experienced a circular vection (CV), whereas nearly all our subjects entered this state.

The succession of two different perceptual states during optokinetic stimulation in our subjects—pattern rotation about the stationary self and self rotation within an apparently stationary environment (CV)—raised the concern that there might be concomitant changes in the way the visual flow is processed, and that these changes might translate into differences in gain or variability. A related and even more important concern is whether measurements obtained while subjects try to estimate the relative rotation of a pattern about themselves can in any way be used to infer how optokinetic and vestibular information interact when the subjects are being rotated within a stationary visual environment, because the subjects' perceptual states are quite different in these two situations. Since most subjects experience the illusion of self-rotation during CV as being quite similar to a real self-rotation, one might suspect that, if at all, only gain measurements obtained during CV can be relevant for the question how visual and vestibular information is combined during self-rotation in condition VO. However, our analysis of intraindividual variability and instantaneous gain obtained in Or90 failed to reveal any differences between the epochs preceding the onset of CV and those following it. The only effect of the occurrence of CV was a transient increase in gain and variability associated with the perceptual 90° interval during which subjects signaled their entering this state, and this effect was observed only during fast rotations. It reflects a brief period of disorientation and disorganization during the transition from one perceptual state into the other which was noticed by most subjects. Also, an interference of the subjects' left hand activation (for signaling CV onset) with the required rapid rate of right-hand signals (90° increments) during fast rotations may have been a factor. In summary, we conclude that the temporal integration of optokinetic signals into a perception of displacement yields identical results independent of whether these signals give rise to a sensation of pattern-in-space rotation or of self-rotation.

Vestibular contribution

With regard to targeting by means of vestibular information only, the present results are in good agreement with an earlier study on vestibular-podokinesthetic interaction

(Becker et al. 2002) which had used similar methods. Noticeably, as in this previous study, the targeting gain did not increase when large displacements were required (cf. discussion below). However, the spread of the G_T curves according to velocity, evident from Fig. 2, V, seems to result to a larger degree from a common temporal process than the spread observed in the previous study. Indeed, when plotted as a function of the time (t) required to reach D_D, the curves of Fig. 2, V, exhibit no differences related to turning velocity in the range $t \leq 15$ s, and a beginning divergence with larger duration can be documented for a few data points only because fast rotations were limited to 15 s.

On the other hand, the velocity spread of the gain curves obtained with incremental indications (Fig. 5, Vr90) agrees with our previous observations also in that it cannot be explained by a common process in the time domain. The conspicuously low gain of the first 90° indication during fast rotations in that condition does not seem to be specific for the vestibular case, because a similar phenomenon was also seen with optokinetic stimulation (Fig. 5, Or90). Note also that the corresponding curves of achieved versus desired displacement (exemplified in Fig. 4A for rotations of 15°/s) exhibit an absolutely regular increase on going from 90° to larger values of D_D. Therefore, the low values of G_I at 90° do not reflect a completely deviating behavior with displacements of this magnitude but merely an initial offset in the process of accumulating angular self-displacement. We can only speculate why such an offset was not seen in our previous experiments; perhaps it is of relevance that D_D=90° was a final target in these experiments rather than just the first of several increments to be signaled.

Because, in our view, the interpretations proposed in our previous report (Becker et al. 2002) essentially also apply to the present data, we here shall comment only on the most important aspects. Most surprising is the consistent observation that targeting gain did not increase with target distance as it would if the information guiding the subjects were characterized by a decay along a time constant (τ) of the order of 15–20 ms (which is a frequently cited value for vestibular behavior; Guedry 1974; Young 1981; Mergner et al. 1996). Also the ability of our subjects to perceptually reach distant targets contradicts the view that their behavior was dictated by a time constant of this magnitude. Indeed, given a value of τ=20 s, displacement perception during, e.g., rotations of 15°/s never could have increased beyond 300° ($\int 15°/\text{s} \cdot \exp(-t/\tau) \cdot dt = 15°/\text{s} \cdot \tau$) and would have required an infinitely long time to reach this value. Other reports touch on the same phenomenon when they relate *under*shoots in vestibular targeting experiments (during rotations: Bakker et al. 1999; Israël et al. 1995; Ivanenko et al. 1997; during passive linear transport: Israël et al. 1997; Mittelstaedt and Mittelstaedt 2001), which reflect an *over*estimation of self-rotation instead of the underestimation expected from the time constant. As an explanation, we have suggested that, in the context of a targeting task, the perception evoked at the onset of a rotation is perpetuated by an extrapolation that fills in for the decaying vestibular signal. To cast this notion into a formal description, we have proposed that a neural integrator of gain $1/\tau$ backs up the dwindling vestibular afferents (Becker et al. 2002) before these are being converted, by a second integrator (that is, by the mechanism of path integration proper) into a perception of angular displacement. A similar idea is the "partial raising" of the time constant by an integrator with a gain of less than $1/\tau$ proposed by Mergner et al. (2000).

The present results corroborate these notions but also hint at the limits of their applicability. Indeed, Fig. 4A indicates that in condition Vr90, even with the lowest velocity, perceptual displacement (abscissa) rose in an approximately linear way with physical displacement (ordinate; recall that the desired displacement can be equated to the perceptually reached displacement). An approximately *constant* rate of perceptual displacement accumulation during most of the trial is also evident from the curves of instantaneous gain in Fig. 5 (panel Vr90). Such a performance is, at least from a formal point of view, correctly rendered by the proposed extrapolating integrator.

On the other hand, the fact that some subjects ceased to indicate further 90° increments after perceptually reaching displacements of, typically, 270–450° during slow rotations, or of 630–810° during 30°/s rotations, warns that vestibular extrapolation cannot be upheld indefinitely, although the point in time where this occurs appears to be idiosyncratic. Conceivably, the perception of a continuing accumulation of angular displacement terminates when subjects become aware of the discrepancy between this perception and the no longer existing (for lack of afferent activation) sensation of turning intensity.

Finally we note that earlier investigations that used repetitive displacement indications to determine the time course of perceived velocity also may have seen responses of the type shown in Fig. 4A but apparently dismissed them as being inconsistent (Guedry 1974; cf. Becker et al. 2002).

Extrapolation: perpetuation of perception arising during initial phase of turning?

Positing, as we did above, that an extrapolation is substituted for the vanishing vestibular signal implies that the perception during the later course of a rotation is determined by the perception arising during the initial phase. The frequent cases of a significant correlation between G_{90} and G_T in the vestibular targeting experiment are compatible with this notion, but they do not prove it. One difficulty with the interpretation of these data is that, being the integral of the internal velocity representation taken across the *whole* trial, the achieved displacement, and hence also G_T, always contains a component reflecting the initial turning perception even if the perception during the later phases of a trial was completely unrelated to its early magnitude.

Of more relevance for the extrapolation hypothesis are the coefficients of correlation calculated for the *instantaneous* gain figures of the repetitive indications experiment. The observation that these coefficients all were significantly different from zero in the vestibular condition (Table 4, Vr90) provides circumstantial support for the notion that extrapolation may have been an important factor in this condition.

On the other hand, the paucity of significant correlation in the optokinetic (Or90) and the combined (VOr90) conditions cannot be taken as proof that extrapolation played no or only a small role when optokinetic information was available. As pointed out in the Results section, the trial-to-trial variations of G_I spanned smaller ranges during Or90 and VOr90 than during Vr90, making the detection of a covariation between early and late parts of a trial less probable. Yet, in view of the low-pass properties of the optokinetic pathway, which allow for a direct estimation of current turning velocity also during the later parts of a trial, it would seem sensible to hypothesize that extrapolation is not required in these conditions. However, a comparison between conditions O and VO (Fig. 2), and likewise between Or90 and VOr90 (Fig. 5), suggests that this view does not hold for the *combined* conditions. Throughout the course of a rotation (Fig. 5) and therefore up to the largest values of D_D (Fig. 2), the gain curves from the combined conditions are fairly independent of the turning velocity and therefore exhibit a clearly smaller velocity spread than those from the purely optokinetic conditions. This observation is difficult to explain without assuming that also here, the decaying vestibular cue is backed up by an extrapolation, or that the perception resulting from the fusion of the vestibular and optokinetic information during the initial phase of the rotation is perpetuated. Otherwise, as the vestibular afferents vanish, the VO and VOr90 gain curves would approach the O and Or90 curves, respectively; that is, the velocity spread of the gain would increase during the course of a rotation. Note that these considerations are valid whatever the exact mechanism (to be discussed below) whereby the combination of V and O improves the gain characteristics over those resulting from monomodal V or O stimulation.

Degraded sensory information: increased importance of cognitive mechanisms

Conditions Oe and VOe were introduced to further pursue the notion that the initial turning perception tends to be carried on during the whole course of a rotation. The *artificial* removal of the optokinetic cue in these conditions deliberately called for a conscious, *cognitive* effort, whereas during the *natural* removal of the vestibular cue (by virtue of its high-pass characteristics) it is not clear whether the hypothesized extrapolation is a conscious or unconscious process. Here, the instructions implied the notion that rotations would continue at *constant* velocity, whereas in the targeting conditions V, O, and VO (and also in Vr90, Or90, and VOr90) we had tried to discourage this notion from determining targeting behavior, by providing subjects with no information regarding the temporal profile of the rotations.

The comparison of panels O and Oe in Fig. 2 demonstrates that subjects were very effective at imagining the continuation of the optokinetic stimulus, the only effects of its disappearance being a slightly larger velocity spread and a very minor increase in intraindividual variability ($\%E_R$). A brief optokinetic stimulus and the subsequent imagination of its further course were also effective in condition VOe in that the gain was maintained at larger values than typical for the monomodal V stimulation (compare panels V and VOe of Fig. 2), and in that variability was reduced although the only available cue for most of the trial duration was the vestibular one. Moreover, the gain curves obtained in condition VOe again suggest that either the vestibular cue was supplemented by an extrapolation or that the initial turning perception was carried on as a whole when subjects aimed at distant targets. Indeed, similar to condition VO, the velocity spread of VOe exhibited no tendency during large displacements to approach the spread seen in condition Oe.

In interpreting the result of conditions Oe and VOe and also of VO we find it useful to conceptually distinguish two processes:

1. An initial build-up of turning perception, including the fusion process. Below we will suggest that already during this process a cognitive “top-down” contribution reflecting past experiences and expectations is invoked and fused with whatever sensory “bottom-up” information is available
2. Perpetuation of the perception established during the build-up phase. This could be achieved either at the level of an internal representation of angular velocity, by carrying on the initial velocity magnitude (or by recreating it as suggested above for the case of the vestibular signal). Alternatively, this process could also take place at a meta-level secondary to the velocity-to-position integration, by perpetuating the initially perceived rate of displacement accumulation. Subjects who, consciously or unconsciously, tried to estimate multiples of the time it took them to perceptually reach the first 90° or 180° displacement obviously used such a strategy.

Clearly, our current data are insufficient to entertain any further conjectures about the possible nature of these processes, and in particular about their temporal structure. Hence, at present we cannot answer the question when build-up is finished and extrapolation starts, although we feel that there may be considerable overlap between the two processes.

Intervention of a "top-down signal": the default velocity

Condition AI of our experiments obviously was the most demanding in terms of the required cognitive involvement, because subjects had to imagine a drum rotation based on a previously established association between (1) the rate at which the pitch of a briefly presented auditory cue changed and (2) the rate at which angular drum position was accumulating. Surprisingly however, although subjects scored self-confidence in this condition significantly worse than in all others, intraindividual variability did not exceed the worst case observed with real stimuli (V). Also, from a *qualitative* point of view, the resulting *pattern* of gain curves was not dramatically different from that of Oe or even of O; in particular there was only a moderate reduction of the gain with increasing magnitude of D_D, suggesting that, also in this condition, the initially established (imaginary) perception was upheld, at least approximately, throughout long-lasting trials.

The one aspect with regard to which AI marks an extreme, though, is the spread of the gain curves according to velocity, which was significantly larger than in any other condition. The graduation of the velocity spread, with largest values during AI and (second largest) Oe, intermediate levels during VOe, O, and V, and a minimum during VO, suggests a common empirical law: the "more" and the "better" the available information, the less the dependence of the gain on turning velocity. More information is available if two cues are combined, hence the smaller spread during VO (or VOr90) as compared to, respectively, V and O (or Vr90 and Or90) and, likewise, during VOe as compared to Oe. Better information is available when subjects can draw permanently on a cue instead of having to imagine it either partly or fully, hence the smaller spreads during V and O as compared to Oe and, worst of all, AI. Leaving aside the question of a more rigorous definition of "more" and "better", the above law is compatible with the following interpretation:

When sensory information becomes degraded, subjects aiming to achieve a desired displacement of given magnitude increasingly tend to deliver their "on-target" signal after a *constant* time, irrespective of v_C, the actual turning velocity; that is, the poorer the available information, the more the subjects' perception is attracted by a fictitious, *fixed* velocity which we will refer to as *default velocity* (v_{def}) in the following. Put into a formal description, this hypothesis states that the subjects' internal representation of the turning velocity (v_{int}) is the weighted average of a real component (v_{sen}) reflecting whatever sensory information is available, and the default velocity:

$$v_{int} = w \cdot v_{sen} + (1 - w) \cdot v_{def} \quad (4)$$

where the magnitude of w ($0 \leq w \leq 1$) depends on how much subjects 'trust" the sensory component. The less confidence that is put into v_{sen}, the smaller the weight w and, hence, the more perception is attracted by the default velocity. Conceivably, this default velocity reflects the subjects' expectation from previous experience, as well as their contextual conjectures.

If we assume, for simplicity, that: (1) subjects feel on target when the condition $\int v_{int} \cdot dt = D_D$ is met, and (2) v_{int} is constant throughout a trial (because its initial value is perpetuated, cf. above), then $D_A = v_C \cdot D_D / v_{int}$; hence:

$$G_T = v_C / v_{int} = v_C / (w \cdot v_{sen} + (1 - w) \cdot v_{def}) \quad (5)$$

With two further simplifying assumptions, namely: (1) on average, v_{sen} correctly signals the actual velocity v_C even if its quality is bad; and (2) v_{def}=30°/s, the velocity spread index defined above (Results) becomes VSI=$(1-w)/(1+w) \cdot 100\%$. Thus, if little confidence is put into the sensory information v_{sen}, VSI will be large and, vice versa, if v_{sen} is judged highly reliable, no velocity spread will occur. Note that by "confidence" we here mean the result of an unconscious evaluation of the current sensory situation rather than the conscious ratings of confidence in own performance delivered after each trial; remarkably, across conditions there was a clear negative correlation between the experimental values of VSI and the mean of these ratings (Table 2).

What actually determines the magnitude of the hypothesized default velocity is an interesting question. We speculate that it is a kind of moving average of recently experienced rotations and therefore reflects a value from the mid-range of the velocities to which subjects are exposed in a given situation (hence the assumption v_{def}=30°/s), but that it is also subject to modification by conscious processes. At any rate, the overestimation of slow and underestimation of fast rotations which we here ascribe to the attraction of perception by a default value is reminiscent of the "range effect" (Poulton 1977) or "contraction bias" (Poulton 1981), which is known to affect many perceptual and psychomotor performances such that responses to stimuli from the low end of the stimulus range become larger than appropriate and those from the high end, smaller.

The scenario described by Eq. 4 must take place early in the course of a trial during the "build-up phase" (see previous section), because in most targeting conditions VSI was fairly similar in long- and short-lasting trials, and because during repetitive indications it was approximately constant over the whole course of a trial, at least with Or90. It must be acknowledged, however, that the vestibular conditions V and Vr90 do not fully conform to this picture, as VSI was a clearly rising function for $D_D \leq 360°$ rather than being similar for all values of D_D. This discrepancy again touches on the question as to how long it takes to build up the velocity signal that ultimately will be extrapolated, and whether the weighting (w) of the sensory afferents is constant or variable during the build up phase. Possibly, in the vestibular conditions the vestibular cue initially was considered highly trustworthy (weight $w \approx 1$); whereas, later on, its weight would be progressively reduced to account for the uncertainty of the central "filling-in" for the decaying peripheral signal.

Fusion of vestibular and optokinetic cues by weighted averaging?

Equation 4 can be interpreted as a rule specifying the *fusion* of sensory with cognitive information by weighted averaging. Could it be that also the fusion of the vestibular and optokinetic cues in conditions VO and VOr90 is based on this principle? Weighted averaging has, in fact, been advocated as a likely mechanism for merging spatial senses (Howard 1997; Zupan et al. 2002) and has been demonstrated in other sensory systems (e.g., fusion of visual and haptic information; Ernst and Banks 2002).

Vestibular and optokinetic information is known to interact already at the level of the vestibular nuclei. This interaction has been viewed as one of complementary, not redundant, signals. With the vestibular cue having high-pass characteristics F and the optokinetic one, low-pass characteristics 1-F, the two cues would simply be added in the vestibular nuclei to yield a broad-band transfer function (Robinson 1977). However, in the present context we certainly are dealing with interactions at higher (cortical) levels, and the general similarity of the gain curves obtained in the V and O conditions, respectively, precludes the notion of complementarity in the frequency domain; rather, it suggests that the two cues provide information that is, at least in part, mutually "overlapping" and, hence, redundant. If so, a fusion by averaging in the time domain would indeed make sense.

Therefore, it is tempting to assume a *common* averaging stage that, at the same time, would fuse the signals from all currently active peripheral sensors as well as the central default signal envisaged above. This view offers a simple explanation of how the weight of the "top-down" component of perception (that is, of the internal default signal) is reduced when the "bottom-up" component draws on an increasing number of sensory channels and, therefore, becomes more reliable. In fact, if there are n active peripheral sensors and, if each input of the averaging stage is given equal weight (a very simplifying assumption), the relative contribution of the default component decreases as $1/(n+1)$, while that of the bottom-up information approaches unity according to $n/(n+1)$. In a follow-up paper dealing with the threefold interaction of vestibular, optokinetic, and podokinesthetic cues, we will show that a simulation based on these considerations can indeed fairly well predict the outcome of the fusion process (Becker, Raab, Jürgens, unpublished work)

Note that, according to our assumptions, when there is only a single velocity or only a small range of velocities, as in the experiments of Bakker et al. (1999), the default velocity will be close to the stimulus velocity so that the mean of the gains recorded in V and in O will differ little from the gain obtained after fusion of V and O. Experiments of this kind therefore fail to detect the top-down contribution and create the impression that fusion is based on a straightforward averaging of only the involved sensory (bottom-up) signals.

The suggestion that the sensory signals contributing to orientation during self-rotation be fused by a weighted averaging that includes a top-down signal (default velocity) can certainly not be refuted on the grounds that the brain was not capable of such an operation. Yet, when weighing possible implementations, several constraints must be kept in mind. For example, the input weights must be controlled by some mechanism to insure that their sum equals unity (normalization). Moreover, a distinction must be made between active input channels that happen to carry a zero signal and inactive ones (signal not existing) which must not be included in the average. Thus, when the optokinetic channel is inactive during darkness, the lack of an optokinetic signal at the input of the averaging stage should not be interpreted as signifying zero velocity, lest we should perceive a self-rotation in darkness as being about half as large as one in a lighted environment.

These constraints could be met by neural networks in which signal magnitude is coded by firing frequency. However, more elegant solutions can be envisaged based on networks using place codes. Spatially coding fusion mechanisms have been suggested, for example, by Ernst and Banks (2002) and Boß et al. (2001). Unfortunately however, the notion of averaging by means of spatially coding networks is at variance with the known physiology of the vestibular and optokinetic systems. The reported activity of single units driven by these systems fits by far better the description of an intensity coded representation of velocity than that of a spatially coded one. Recordings in monkey from the vestibular areas of the brain stem (Buettner et al. 1978; Waespe and Henn 1979), the thalamus (Büttner et al. 1977), and the cortex (Akbarian et al. 1988; Büttner and Buettner 1978; Grüsser et al. 1990a, 1990b; for a review, see also Fukushima 1997) all suggest that the magnitude of the vestibular and optokinetic velocities is represented by the number and the firing frequency of responsive neurons rather than by the neurons' relative location in these areas. It is only after the transformation of vestibular velocity signals into representations of an animal's angular *position* that place codes make their appearance, mostly in limbic structures (head position cells in rat thalamus: Taube 1995; lateral mammillary nuclei: Stackman and Taube 1998; post-subiculum: Taube et al. 1990; retrosplenial cortex: Cho and Sharp 2001; and in monkey presubiculum: Robertson et al. 1999). However, there is no evidence for separate representations of angular position according to the source of the velocity signal that was integrated (optokinetic, vestibular, arthrokinetic, etc.) that could serve as input stages for a fusion network using a place code. Because, moreover, the sensation of being rotated during VO trials (and during any rotation within a visually structured environment in general) is a unitary one which does not allow a distinction between an optokinetic and a vestibular velocity, fusion is more likely to occur in the velocity domain rather than at the level of position representation.

In an investigation of vestibular–podokinesthetic interaction using very similar methods as the present study (Becker et al. 2002), we also have observed the phenomenon of a velocity spread of the gain curves during monomodal stimulation and its reduction upon combination of two sensory channels. Similarly as above, these observations led us to suggest that the monomodal perceptions were biased in favor of a default value reflecting previous experience and expectations, and, furthermore, to conclude that the gain during bimodal stimulation cannot result from a straightforward averaging of the monomodal gains. Different from what we suggest here, however, we then have explained the reduction, or virtual disappearance, of the velocity spread during combined stimulation in terms of a model of vestibular–proprioceptive interaction that invokes an *eigen*model of the vestibular channel (Mergner et al. 1991). An analogous explanation for the fusion of vestibular and optokinetic information in the present experiments is difficult. Skipping much of the pertinent arguments, we only mention that, according to this model, there should be no velocity-related variations of the gain during optokinetic conditions, a prediction which is clearly in conflict with the experimental evidence. Vice versa, however, the notion of averaging with inclusion of a top-down default component might offer an alternative explication for the results observed with vestibular-podokinesthetic interaction and thus allow for a conceptual generalization of sensory fusion for arbitrary combinations of sensory channels. This is not to say that *eigen*models do not play an important role for the perception of self-rotation. On the contrary, they appear to be vital for the identification of the scenario into which the subject is embedded (answering questions such as: "Am I on firm or on moving ground?") and, hence, instrumental in understanding the phenomenon of circular vection and other illusions. Future work will have to examine whether the notions of: (1) weighted averaging of multiple, partially redundant, sensory and "top-down" information; and (2) interaction of complementary sensory information by way of an *eigen*model, can be merged into a unifying picture of human turning perception.

Conclusion

The experimental evidence we have presented (1) contradicts the notion that the vestibular and optokinetic cues which guide human navigation during horizontal rotations of constant velocity be fused by straightforward averaging, and (2) suggests that cognitive mechanisms are an important component of navigation. One facet of this cognitive involvement, the ability to extrapolate, is readily appreciated by inspection of the data and taking into account the experimental conditions, although nothing certain can be said about the level of processing at which it takes place. The second facet, the intervention of a "default" velocity, is, for the time being, a construct introduced to arrive at a unifying description of the data and, in particular, of the mechanism whereby vestibular and optokinetic information is combined for the purpose of navigation under the conditions of our experiments. Clearly, our contention that it reflects a priori knowledge, past experience, and expectations calls for direct experimental corroboration. Also, we are aware of the fact that the explanatory power of the hypothesized combination of bottom-up "real" information with top-down "default" information rests on many simplifications and covers only the general picture emerging from our data, without accounting for every detail. However, as far as the experimental design is concerned, we hold that the use of rotations of constant velocity was not an undue oversimplification but is of practical relevance, because many traffic situations consist of phases of acceleration followed by epochs of more or less constant linear and/or angular velocity. Applied to these situations, the concept discussed above would suggest that there is a strategy to monitor closely and make full use of sensory information only at the beginning of such periods, and then to switch to extrapolation in order to free processing resources for other purposes.

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