

Vestibular Perception and Navigation in the Congenitally Blind

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¹Department of Movement and Balance, Division of Neurosciences and Psychological Medicine, Imperial College, Charing Cross Hospital, London, United Kingdom; and ²Center for Sensorimotor Research, Julius Bernstein Center for Computational Neuroscience, Department of Neurology, Ludwig-Maximilians-Universitaet Muenchen, Munich, Germany

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Seemungal BM, Glasauer S, Gresty MA, Bronstein AM. Vestibular perception and navigation in the congenitally blind. *J Neurophysiol* 97: 4341–4356, 2007. First published March 28, 2007; doi:10.1152/jn.01321.2006. Vestibular input is required for accurate locomotion in the dark, yet blind subjects' vestibular function is unexplored. Such investigation may also identify visually dependent aspects of vestibular function. We assessed vestibular function perceptually in six congenitally blind (and 12 sighted) subjects. Cupula deflection by a transient angular, horizontal acceleration generates a related vestibular nerve signal that declines exponentially with time constant $\approx 4\text{--}7$ s, which is prolonged to 15 s in the evoked vestibular-ocular reflex by the brain stem "velocity storage." We measured perceptual velocity storage in blind subjects following velocity steps (overall perceptual vestibular time constant, *experiment 1*) and found it to be significantly shorter (5.34 s; range: 2.39–8.58 s) than in control, sighted subjects (15.8 s; $P < 0.001$). Vestibular navigation was assessed by subjects steering a motorized Bárány-chair in response to imposed angular displacements in a path-reversal task, "go-back-to-start" (GBS: *experiment 2*); and a path-completion task, "complete-the-circle" (CTC: *experiment 3*). GBS performances (comparing response vs. stimulus displacement regression slopes and r^2) were equal between groups ($P > 0.05$), but the blind showed worse CTC performance ($P < 0.05$). Two blind individuals showed ultrashort perceptual time constants, high lifetime physical activity scores and superior CTC performances; we speculate that these factors may be inter-related. In summary, the vestibular velocity storage as measured perceptually is visually dependent. Early blindness does not affect path reversal performance but is associated with worse path completion, a task requiring an absolute spatial strategy. Although congenitally blind subjects are overall less able to utilize spatial mechanisms during vestibular navigation, prior extensive physical spatial activity may enhance vestibular navigation.

INTRODUCTION

How do blind subjects navigate within the world? When sighted subjects walk in the dark, they are able to derive their location via a process called *path integration* in which position is derived from inertial vestibular and haptic signals via mathematical integration and vector addition (Mittelstaedt and Mittelstaedt 1980). Haptic input is sufficient to inform the path integration process for sighted subjects during translational movements in the dark; however, only vestibular input adequately updates position when subjects make walking turns (Glasauer et al. 2002). Despite this we know virtually nothing about vestibular function in the congenitally blind.

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Navigation capacity of the congenitally blind during walking

Navigational performance in the congenitally blind during locomotor tasks, for which there is abundant data (Loomis et al. 1993; Thinus-Blanc and Gaunet 1997), may indirectly reflect vestibular function in this group. During *route navigation* tasks, i.e., re-tracing a previously walked route (viz. path reproduction/reversal), congenitally blind and sighted subjects display equivalent performance (Rieser et al. 1986; Loomis et al. 1993; Thinus-Blanc and Gaunet 1997). Route navigation mechanisms rely on a representation of the "path structure" (e.g., 2 steps ahead, 90° right turn, etc.) without reference to external landmarks (Bigelow 1991; Foulke 1982; Lederman et al. 1985). During *inferential tasks*, i.e., tasks requiring the derivation of novel spatial relationships from previously experienced spatial measures (e.g., path completion of the last leg of a triangular circuit), congenitally blind subjects show a decrement in performance compared with sighted subjects in most, but not all, studies (Loomis et al. 1993; Rieser et al. 1986; Thinus-Blanc and Gaunet 1997). If these findings reflect vestibular function in the congenitally blind, then they suggest that perception of vestibular signals is intact in this group although the relative failure in "inferential" navigational tasks may imply a deficit in the utilization of this information during navigation.

Isolation of vestibular signal during angular reorientation (vestibular navigation)

Walking tasks, however, tell us little about the vestibular contribution in blind subjects because vestibular and haptic signals cannot be isolated during locomotion. Navigation tasks that isolate vestibular input, called vestibular navigation, have demonstrated that humans can orient using only vestibular signals (Israel et al. 1995, 1996; Metcalfe and Gresty 1992; Siegler et al. 2000; von Brevern et al. 1997). These tasks consist of passive subject displacement (stimulus) in the dark while sitting on a rotating chair. Subjects effect a return to origin (response) using a manual device linked to the motorized chair. We thus tested "homing" ability during angular vestibular navigation for path reversal (*route navigation*) and path completion (*inferential navigation*) tasks in sighted and congenitally blind subjects.

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Comparing path reversal and path completion during vestibular navigation

The comparison between path reversal and completion tasks may allude to the mechanisms employed during angular vestibular navigation. The use of a single mechanism for both tasks, e.g., a continuously updated heading (Ivanenko et al. 1997), during whole-body rotations, i.e., an “internal compass,” should give similar performances between tasks. Theoretically, accurate path reversal performance could be independent from calibrated spatial representations because accurate reproduction of the perceived stimulus angle, however erroneously perceived, will result in accurate performance and sighted subjects can accurately recover an inertially perceived displacement by reproducing motion dynamics (Israel et al. 1997) obviating spatial mechanisms. In contrast, during angular path completion, subjects are obliged to convert motion-dynamic signals to position and utilize a calibrated spatial mechanism. In this case, if subjects possess an erroneous internal calibration of vestibular-derived position, then their path completion performance will be poor. Thus by comparing performance differentials between angular path reversal and path completion tasks, we will analyze the use of such spatial mechanisms distinct from an ability to accurately perceive vestibular signals.

Factors influencing congenitally blind subjects' navigation

The inconsistency in the literature regarding blind versus sighted subjects' navigational capacity may be related to individual subject differences (Loomis et al. 2001; Thinus-Blanc and Gaunet 1997). We assessed two factors: the vestibular time constant obtained via a perceptual method and the lifetime spatial experience of the blind volunteers via questionnaire.

The overall time constant of a vestibular response depends primarily on both peripheral (cupula) and brain stem (velocity storage) components. Following a yaw-axis angular velocity step (to the head), elastic forces exponentially restore the cupula to its resting position with a time constant estimated to be between 4 and 7 s (Büttner and Waespe 1981; Dai et al. 1999; Gizzi and Harper 2003). Velocity storage improves the low-frequency yaw-axis rotational response of the cupula output by prolonging the vestibular response, e.g., vestibuloocular reflex (VOR) nystagmus slow phase, which declines with time constant of circa 15 s after an abrupt acceleration (Blair and Gavin 1981; Büttner et al. 1978; Cannon and Robinson 1985; Raphan and Cohen 1977, 1979; Robinson 1977; Solomon and Cohen 1992a,b). Thus changes in the duration of the vestibular time constant (primarily effected by changes in the velocity storage component) could potentially influence the accuracy of vestibular signal transduction including the duration of postrotational vestibular sensation. Vestibular sensation and VOR are different outputs albeit of the same underlying vestibular signal, but early data regarding the correspondence between perceptual and VOR time constants in the yaw plane were inconsistent, probably due to unreliable recording techniques (reviewed by Jongkees 1974). Also, both perceptual and VOR time constants can be context dependent (Chan and Galiana 2005; Grunfeld et al. 2000), thus interstudy comparisons may be misleading. Okada et al. (1999), using *simultaneous* measurement of oculomotor and perceptual measures of the ves-

tibular time constant, showed a good correlation between VOR and perception. Because one of our aims was to assess factors influencing the cognitive task of vestibular navigation, we assessed the perceptual time constant as opposed to the VOR time constant as it was of greater relevance.

Effect of congenital blindness on vestibular processing—the velocity store mechanism

Abnormalities of the vestibular time constant in congenitally blind subjects could thus allude to a related question: is the emergence and maturation of the velocity store mechanism visually dependent? The velocity store mechanism undergoes visually mediated postdevelopmental plasticity as demonstrated in patients with excessive retinal slip who show attenuated time constants (Grunfeld et al. 2000; Okada et al. 1999). Human neonates' velocity storage mechanism is underdeveloped but reaches adult values by 2 yr (Ornitz et al. 1985; Weissman et al. 1989), suggesting its visually dependent maturation, a conclusion supported by animal visual-deprivation studies (Harris and Cynader 1981; Tusa et al. 2001). There is, however, no quantitative data regarding vestibular reactions in congenitally blind patients (Forssman 1964; Graybiel 1970; Sherman and Keller 1986). We tested the hypothesis that the human vestibular storage mechanism is visually dependent with a technique (Okada et al. 1999) that permits vestibular time constants to be estimated in patients such as the congenitally blind in whom there is no coordinated eye movement (Kompf and Piper 1987; Sherman and Keller 1986).

In summary, we sought to determine whether blind subjects' vestibular navigatory capacity is equivalent to that of sighted subjects, the velocity storage mechanism, measured perceptually, is present in congenitally blind subjects and thereby whether its emergence is dependent on vision; and lifetime exposure to physical activity affects vestibular perceptual function in congenitally blind subjects.

METHODS

Experiment 1: perceptual vestibular time constant

SUBJECTS. We tested five congenitally blind subjects (subjects B2–B6; B1 was lost to follow-up; Table 1). Normative data from 31 sighted subjects has been previously published (Okada et al. 1999).

APPARATUS, PROTOCOL, AND ANALYSIS. Subjects indicated their perceived instantaneous angular velocity of whole-body rotation; the apparatus (Fig. 1A) has been described in detail elsewhere (Okada et al. 1999). In summary, subjects were rotated (yaw-axis) at a constant velocity of 90°/s in the dark with sound masking in a Bárány chair (with a padded head rest and under infra-red video monitoring) for 1 min then suddenly stopped, resulting in a sensation of self-rotation (in those with intact vestibular function) in a direction opposite to that of initial chair rotation. Subjects were instructed to turn a chair-mounted hand-wheel at an angular velocity proportional to their perceived self-rotation. The wheel's central spindle drove an on-axis tachometer (British Encoder Products, UK) the voltage output of which was proportional to the angular velocity with which it was turned. Four stopping responses were obtained per subject. The hand-wheel tachometer output was digitized at 250 Hz, and an exponential curve was fitted to the falling portion of the obtained output (shown in Fig. 1B) via a least-squares exponential fitting algorithm (goodness of fit assessed using r^2). Specifically, a straight line was fitted (via least-squares method) to the natural logs of the means of successive 250-ms

TABLE 1. *Subjects' characteristics and physical activity scores*

Subject	Age, yr	Sex	Age and Cause of Blindness	Employment	Physical Activity (Period of Activity), yr	Activity Score*
B1	50	F	Birth, retrolental fibroplasia	Telephonist	Physical education (<10–16)	2
B2	42	M	Birth, micro-ophthalmia	Telephonist	Blind cricket (11–16)	3
B3	39	F	<10 months, retinoblastoma	Welfare rights worker	Water skiing, dancing (34–present)	3
B4	35	M	<10 months, retinoblastoma	Musician (drummer)	Blind cricket, football (<10–16), music (11–present)	8
B5	26	M	Birth, glaucoma	Sales manager	Blind cricket, bowling (25–present)	2
B6	39	F	<10 months, retinoblastoma	Physiotherapist	Judo, goalball (<10–19), skiing (17–19; 29–present)	9

Duration of Activity (0–3; 1 Point for Each Epoch)	Subjective Report of Sporting Ability (0–3)	Degree of Vestibulo-Spatial Activity (0–3)
<10	Poor	Very little or None
11–18	Average	Some
>18	Above average	Medium
	Very good	Great deal

All subjects had orientation and mobility training at 10–11 years of age. *Activity scoring schema

blocks of the tachometer signal with the slope of this plot providing the exponential time constant. Although the vestibular response is comprised of mainly two time constants, these can be approximated by a single time constant as previously used for the measurement of vestibular perceptual (and VOR) responses (Merfeld et al. 2001).

Experiments 2 and 3: vestibular navigation ("self-rotation test")

SUBJECTS. We tested six congenitally blind (38 ± 8 (SD) yr; Table 1) and 12 sighted subjects (30 ± 10 yr). We also tested two patients with acquired complete vestibular loss as controls to assess any somatosensory contribution to vestibular navigation.

APPARATUS. The subjects sat on a vibration-free rotating chair (Contravez; torque 120 Nm) in the dark with white-noise sound masking via earphones (Fig. 2A). The experimenter observed the subject at all times via infrared video camera. The chair could be rotated by external computer control (stimulus) or the subject could actively rotate himself by manipulating a directionally congruent joystick that provided a velocity demand to the servo-motor (response).

EXPERIMENTAL PROTOCOL AND INSTRUCTIONS. The highly responsive nature of the chair to joystick deflection necessitated an initial sufficient period of free practice during which only subject-driven chair rotations were made (≈ 15 min; without visual, auditory cues or other indication of performance). During free practice, the maximum joystick-driven angular velocity was incrementally increased from 20 to 140°/s. Subjects were informed of each incremental increase in joystick gain and were encouraged to explore the new limits of the joystick-driven dynamic range, and this was monitored on infrared camera. Subjects proceeded to the practice experiment stage once they were able to confidently use the joystick at the maximum setting (i.e., the experimental setting of peak 140°/s).

The conditions and stimuli (see next paragraph for conditions and stimuli) were identical between practice and formal experiments (again without visual or other feedback) except that there were half the number of stimuli per condition in the practice session (right and left stimulus directions were balanced in the formal experiment but not in the practice). The practice experiment phase took 15 min. During the practice experiments, subjects were told to decide on a strategy for each task and then to use this consistently in the formal experimental session (this approach was used to explore the natural repertoire of strategies employed by subjects).

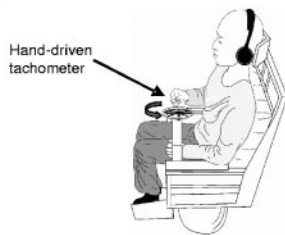
After practice experiments, subjects then performed formal experiments. Experimental rotational stimuli, consisting of externally imposed, computer-controlled, angular displacements were followed by subjects' responses i.e., joystick-controlled rotations, under two conditions (see *Conditions*). Stimuli consisted of raised cosine velocities with maxima 30, 60, 90, and 120°/s, durations of 1–6 s (peak acceleration range: 16–377 °/s²) and displacement range of 15–360° in both directions giving 48 different stimuli presented in a random order. Subjects were informed that the largest displacement stimulus was 360°. The large number of stimulus profiles counteracted "counting" strategies for replicating stimulus motion duration. Stimulus dynamics were selected with the limitations imposed by the dynamic response range of the semi-circular canals in mind, thus the maximum stimulus displacement of 360° remained within the optimal frequency range (i.e., 0.167 Hz) of the semi-circular canals (Mayne 1974). A maximum response chair angular velocity of 140°/s was employed that, in addition to adequate practice (see preceding text), ensured that subjects' responses were also within the optimal semi-circular canal frequency range. The maximum stimulus angular acceleration was 377°·s⁻¹·s⁻¹ compared with the maximum response acceleration of 2,000°·s⁻¹·s⁻¹.

CONDITIONS. *Experiment 2.* In a "go-back-to-start" condition (GBS, Fig. 2B), subjects were passively rotated to a discrete angular position (left or right 15–360° from the origin) and instructed to return actively to the start position as accurately as possible, by moving in the opposite direction to the stimulus movement.

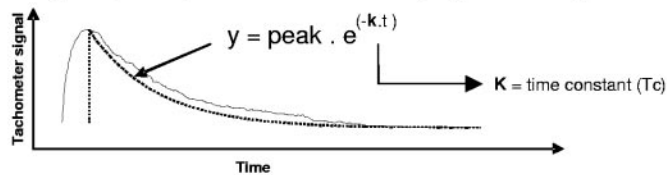
Experiment 3. In a "complete-the-circle" condition (CTC, Fig. 2C), subjects were passively rotated to a discrete angular position (15–360°). Subjects were instructed to arrive back at the start position as accurately as possible following the stimulus rotation by continuing in the same direction to the start position, i.e., by completing the circle. The ability to complete the circle requires converting the stimulus dynamics into position and then navigating to the start using only a position strategy. They were told not to respond in the CTC condition if they perceived a 360° stimulus. *Experiments 2 and 3* utilized the same repertoire of (randomized) stimulus rotations. In addition, the conditions were split into two blocks of 24 stimuli each and interleaved with a balanced order of presentation between GBS and CTC between subjects (e.g., GBS-CTC-GBS-CTC vs. CTC-GBS-CTC-GBS).

DATA RECORDING AND PROCESSING. The chair tachometer (velocity) output was recorded at 250 Hz and analyzed off-line. Angular displacement was obtained by integrating the velocity trace and

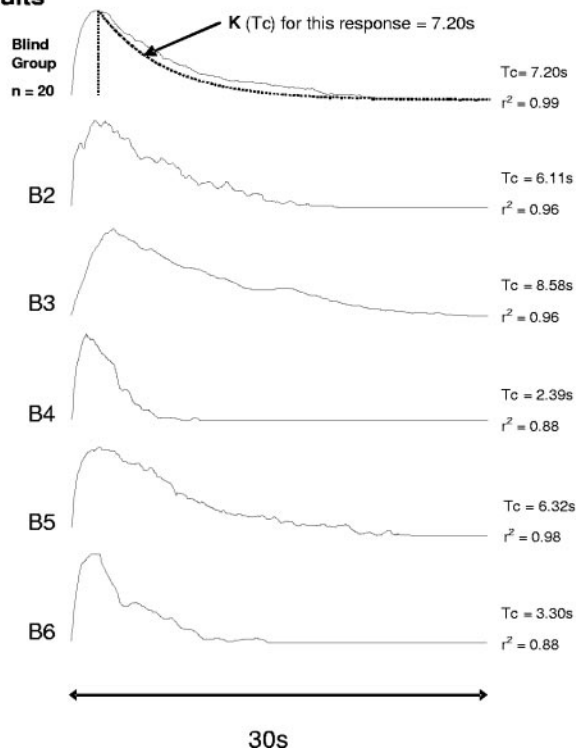
A Apparatus



B Obtaining the perceptual time constant (T_c) from subjects' responses



C Results



movement duration obtained directly from the record (Fig. 2B). To obtain peak angular acceleration, the velocity waveforms were smoothed using a five-point moving average smoother and rectified, differentiated, filtered using a predictive finite impulse response median hybrid filter (PFMH) (Heinoven and Neuvo 1988), and rectified. Finally, peak angular acceleration was measured from the maximum of the resulting trace (Fig. 2B).

DATA ANALYSIS. Displacement performance. Quantitative analysis of displacement performance was obtained by linear regression between response and stimulus displacements. Regression slopes of GBS and CTC were compared using a two-tailed *t*-test, and correlation coefficients were compared using Fisher's *r*-to-*z* transformation.

Variability of within-subject responses was gauged using a group analysis of individuals' regression residuals. Specifically, for each stimulus angle, the expected response (obtained from an individual's regression equation) was subtracted from the observed angular response. Because each subject's residuals were normalized to their own

FIG. 1. A: apparatus used for obtaining the perceptual vestibular time constant. The chair-mounted tachometer was turned by subjects in accord with their perceived self-rotation. B: y axis of perceptual (tachometer) responses (grand average of blind responses is shown here and in the following figures) were expressed in arbitrary units and normalized by their maximal (100%) amplitude. The time constant (k in figure) was obtained by fitting a single exponential to the obtained perceptual response from the peak signal as shown. The initial rising phase of tachometer output from 0 to maximum was not used in obtaining the time constant. C: averaged records of all perceptual velocity responses were obtained to assess the mean vestibular time constant for 5 blind subjects and for each subject individually ($n = 4$ recordings/subject).

regressions, the task-specific grouped residuals gave an estimate of the overall within-subject variability for each group and task. We compared group residuals (i.e., a four group comparison: sighted GBS, sighted CTC, blind GBS, and blind CTC) using univariate ANOVA. Post hoc comparisons were obtained using Scheffe's test.

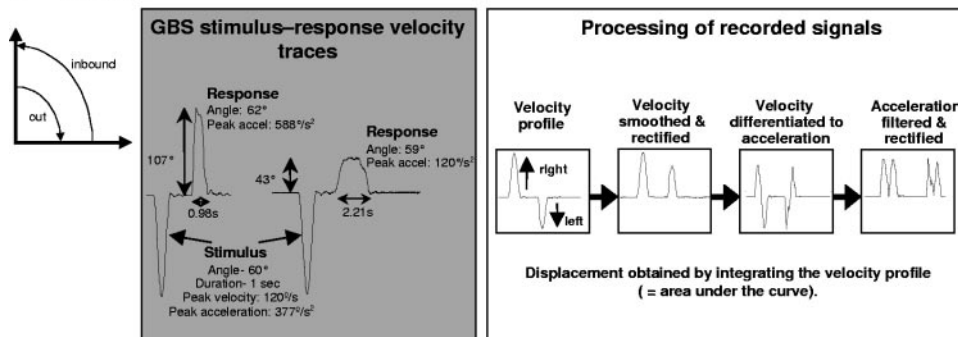
Navigational strategy. Although task performance was measured according to subjects' angular response accuracy, an analysis of navigational strategy was important since subjects could be accurate in the task by reproducing the motion profile of their sensed motion (termed topokinetic navigation by Berthoz 1997) rather than relying on a sense of position to guide their response. Navigational strategy was assessed qualitatively and quantitatively.

Qualitative assessment was based on observation of the chair angular velocity records as shown in Fig. 2B; i.e., reproduction of stimulus velocity profile (Fig. 2B, left trace in gray panel) versus matching stimulus displacement without reproducing stimulus kinetics (Fig. 2B, right trace in gray panel).

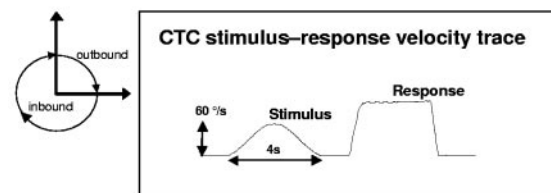
A Apparatus



B GBS



C CTC



Multiple regression analysis was used to quantify subjects' strategy in vestibular navigational tasks (Israël et al. 1996). In general, multiple regression provides information about the relationship between several predictor variables and a dependent variable. For our purposes, we were interested in the relative contributions of the various stimulus parameters (i.e., stimulus angle, peak velocity, peak acceleration, and motion duration) to the subjects' task performance, that is, response displacement. In summary, we used multiple regression to determine subject strategy by identifying the stimulus parameters that most predicted response displacement. We separately assessed subjects' perceptual encoding of stimulus peak velocity using multiple regression analysis (with stimulus displacement, time, peak velocity, and peak acceleration as independent variables). We similarly assessed the perceptual encoding of stimulus peak acceleration and motion duration.

Physical activities of daily living (ADL) scores

Blind subjects were questioned with respect to lifetime physical ADLs (see scoring - Table 1, bottom). Duration of physical activity was divided into three epochs; <10, 11–18, and >18 yr. One point was given for reported regular (> 1/wk) physical activity in each epoch. Subjects rated themselves in terms of sporting ability relative to their blind peers as poor (0 points), medium (1 point), good (2 points), or exceptional (3 points). Subjects were ascribed scores for the type of activities in which they participated. More points were

awarded for those activities requiring whole-body spatial re-orientation, which we termed as vestibulospacial activities (e.g., alpine skiing, 3 points). Sports requiring minimal whole-body re-orientation scored less, e.g., blind cricket (1 point) in which body position is often kept as static as possible and requires primarily coordination between hand and auditory cues since the target (a ball) always comes from the same location.

RESULTS

Experiment 1: perceptual velocity time constant

Blind subjects' mean perceptual time constant was 7.23 s as measured by exponential fit ($r^2 = 0.99$) of the grand average (Fig. 1, B and C, blind group). Individual time constants ranged from 2.39 to 8.58 s (Fig. 1C) with a mean of 5.34 ± 2.50 (SD) s. Normative data for 31 sighted subjects has been previously obtained in our laboratory (Okada et al. 1999) with a mean overall perceptual time constant of 15.8 ± 7.7 s, which was significantly longer than that of the blind group ($P < 0.001$; independent *t*-test).

The physical ADL (activity scores) of the blind subjects are presented in Table 1. The two subjects possessing the highest scores in the lifetime physical ADL score, i.e., B4 and B6, also

FIG. 2. A: apparatus used for the self-rotation test. Chair rotation (left or right) was controlled by a directionally congruent joystick. B: plan view showing a schematic of the task required by subjects in go-back-to-start (GBS) and typical recorded chair velocity traces. Two traces shown in the gray box represent the 2 broad types of strategy used; i.e., matching the velocity profile of the stimulus (left trace) or matching the displacement of the stimulus only (right trace). In accordance with convention, upward and downward deflections on the velocity recordings were respectively rightward and leftward rotations. For ease of comparison, velocity and acceleration profiles were rectified. C: plan view showing schematic of the CTC task. The chair velocity recording shown is typical for all 18 subjects and indicates a spatial (position-based) strategy.

displayed the shortest time constants; viz. *B4*, 2.39s and *B6*, 3.30s.

Experiment 2: path reversal task (GBS)

SIGHTED SUBJECTS. *Sighted subjects: GBS displacement performance (response angle vs. required angle).* Sighted subjects were highly consistent in reproducing the angular displacement with a cumulative regression analysis between response (*R*) and stimulus displacements (*S*) of all data points from all sighted subjects ($n = 561$) yielding $R = 0.76 S + 31^\circ$ and r^2 of 0.80. Figure 3 (*top left graph*) shows the regression plot between response and stimulus displacements for the average of all response data points for each particular stimulus angle for the sighted group. Individual performances (Table 2, *Displacement Performance* for subjects *S1–S12*) were similarly consistent with r^2 for linear regressions between response and stimulus displacements ranging from 0.75 to 0.94 ($P < 0.0001$ for all).

GBS strategy. Inspection of the response velocity traces demonstrated two types of strategy: a kinetic matching strategy (i.e., velocity matching as in Fig. 4A, or velocity and accel-

ation matching as in Fig. 4B) or a displacement matching strategy (Fig. 4C). Overall group strategy was quantified by multiple regression analysis ($n = 561$) of the combined responses (Table 3; line labeled sighted) with response angle being the dependent variable and stimulus displacement, peak velocity, duration, and peak acceleration as predictors. This analysis showed stimulus angle to be the most important predictor of response angle ($\beta = 0.75$; $P < 0.0001$; Table 3). Stimulus peak velocity ($\beta = 0.20$; $P < 0.05$) and acceleration ($\beta = -0.14$; $P < 0.01$), but not stimulus duration, were also significant predictors for response angle. Overall the sighted group reproduced a stimulus displacement by matching both positional (displacement) and kinetic (velocity and acceleration) components (Table 3). Individuals' strategy is summarized in Table 2, *Predictors of Response Angle* for subjects *S1–S12*.

There was a good agreement between visual inspection and regression methods in assessing strategy. Thus comparison between Fig. 4A (visual inspection) and multi-regression data for *S10* (Table 2, right-hand side, data for *S10*) shows that *S10* matched stimulus peak velocity but not peak acceleration. Similarly *S2* matched the kinetics of angular motion (compare Fig. 4B and Table 2, right-hand side, data for *S2*), whereas *S9*

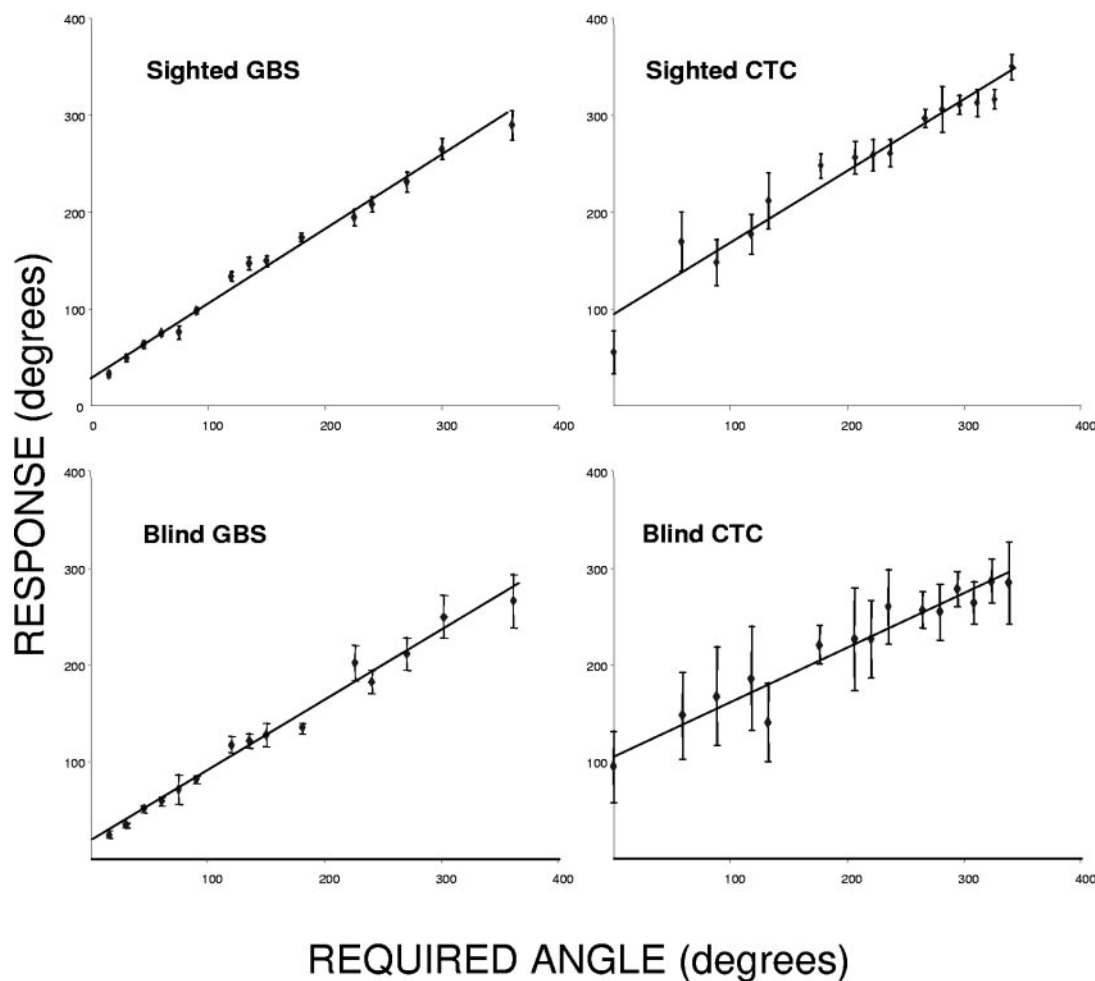


FIG. 3. Absolute angular responses for the self-rotation test. Average response angle from all subjects (y axis, degree) vs. required angle (x axis, degree) for sighted and blind GBS and complete-the-circle (CTC, as labeled; error bars display SE). The GBS regression slopes of averaged responses for sighted and blind subjects were not significantly different. Regression slopes of averaged responses for CTC were significantly different between blind and sighted groups.

TABLE 2. Individual performance and strategy

Subject Number, Sex & Age	Displacement Performance for GBS and CTC Linear Regression-Response vs. Stimulus Angle				Predictors of Response Angle for GBS* Multiple Regression for GBS-Response Angle vs. Stimulus Angle, Velocity, Time, Acceleration					
	GBS- Angle		CTC- Angle		Multiregression Fit		Angle (1)	Velocity (0.41)	Time (0.49)	Accel (0.07)
	r^2	B	r^2	B	n	r^2	β	β	β	β
S1 (F - 26)	0.90	1.0	0.18 ^ψ	0.45 ^ψ	48	0.81	0.57 ^ψ		0.34 ^ψ	
S2 (M - 24)	0.83	0.76	0.79	0.85	48	0.88		0.72	0.38 ^τ	-0.39 ^τ
S3 (F - 26)	0.92	0.83	0.74	0.68	48	0.93	0.68	.29 ^ψ		
S4 (M - 55)	0.82	0.61	0.55	0.81	48	0.83	0.49 ^ψ	.40 ^ψ		
S5 (M - 39)	0.80	0.63	0.69	0.72	47	0.82	0.70 ^τ			
S6 (F - 24)	0.94	1.0	0.80	0.93	43	0.94	1.00			
S7 (M - 23)	0.89	0.83	0.72	0.84	48	0.90	0.69			-0.23 ^ψ
S8 (M - 22)	0.74	0.78	0.06	0.24	48	0.78	0.60 ^ψ			-0.36 ^τ
S9 (M - 22)	0.90	0.74	0.66	0.74	47	0.90	0.78			
S10 (M - 35)	0.79	0.55	0.02	0.11	48	0.81		0.48 ^ψ		
S11 (M - 34)	0.75	0.58	0.55	0.54	48	0.84		0.71 ^τ		-0.32 ^ψ
S12 (M - 25)	0.90	0.74	0.67	0.97	48	0.90	0.86			
B1 (F - 50)	0.73	0.90	0.27	0.82	48	0.74	1.2			
B2 (M - 42)	0.74	0.63	0.22 ^τ	0.49 ^τ	48	0.79		.73 ^τ		-0.44 ^ψ
B3 (F - 39)	0.71	0.47	0.00	0.04	47	0.73	**			
B4 (M - 35)	0.88	0.81	0.77	0.60	48	0.90	.68 ^τ	0.39 ^ψ		-0.30 ^ψ
B5 (M - 26)	0.61	0.71	0.27	0.46	48	0.63	**			
B6 (F - 39)	0.93	1.0	0.90	0.98	48	0.95	1.2		-0.26	
L1 (M - 55)	0.19	0.79			48	0.15				
L2 (F - 58)	0.18	0.01			48	0.45				

Linear and multiple regressions for individual data viz. correlation coefficients (r^2), and slopes, both standardized (β) and un-standardized (B) ($P < 0.0001$ for all except $\psi = P < 0.05$, $\tau = P < 0.01$; non-significant values i.e., $P > 0.05$, are omitted). Shown in brackets under each of the "Predictors of response angle for GBS" are the inherent correlations of the stimulus angle set, i.e., r^2 of stimulus angle vs. each other stimulus parameter (e.g., under "velocity", $r^2 = 0.41$ for stimulus angle vs. stimulus peak velocity). * "Predictors of response angle" refer to go-back-to-start (GBS) only since only a position strategy was used in complete the circle (CTC). GBS strategy is shown by the reported β values under the respective columns e.g., a spatial strategy was signified by high β values in the "Angle" column as in S5. **B3 and B5 respective GBS strategies were best described as displacement matching since, although multiple regression analyses did not yield any significant β values, those for angle approached significance, i.e., $P < 0.08$). Letter designation for subjects denotes S for sighted, B for blind, and L for labyrinthine deficient. Letter and number in parentheses refers to gender and age in years.

matched only stimulus displacement and not dynamics (compare Fig. 4C with Table 2—data for S9). In summary, sighted subjects demonstrated a variety of strategies (position-based and kinetic-matching) with similar consistency in returning to origin in the GBS task (path reproduction).

GBS encoding of velocity, acceleration, and motion duration. A multiple regression analysis (with stimulus displacement, peak velocity, duration, and peak acceleration as the independent variables) for sighted group data showed that response peak velocity was dependent on stimulus velocity ($\beta = 0.42$; $P < 0.0001$), acceleration ($\beta = 0.27$; $P < 0.0001$), and displacement ($\beta = 0.24$; $P < 0.05$). Response acceleration, however, was dependent on stimulus acceleration only ($\beta = 0.84$; $P < 0.0001$). Response motion duration was dependent on stimulus duration ($\beta = 0.58$; $P < 0.0001$), stimulus velocity ($\beta = 0.22$; $P < 0.01$), and inversely dependent on stimulus acceleration ($\beta = -0.27$; $P < 0.0001$) but not stimulus displacement ($P = 0.6$). Table 4 shows the results of analyses for individuals' data with respect to predictors of stimulus kinetics; note that in the sighted group, the only parameter that significantly predicted response peak angular acceleration was stimulus peak angular acceleration. In contrast, response peak angular velocity (Table 4, left) was predicted by other variables apart from peak stimulus angular velocity. This implies that peak head angular acceleration was encoded as a distinct representation separate from peak head angular velocity.

BLIND SUBJECTS. Group GBS displacement performance (response angle vs. required angle). The blind group's GBS performance ($R = 0.74 S + 17^\circ$; $r^2 = 0.77$; $n = 287$) was not significantly different ($P > 0.05$) from the sighted for slope (t -test) and r^2 values (Fishers r' transformation) for their respective regressions between response (R) and stimulus displacements (S) of all data points from all blind subjects. The GBS y intercept was however, larger in the sighted group compared with blind (31 vs. 17° ; $P < 0.01$; unpaired, 2-tailed, t -test). Figure 3 (bottom left) shows the regression plot between response and stimulus displacements for GBS for the average of all response data points for each particular stimulus angle for the blind group. [Nb: positive y intercept values are mainly due to "regression to the mean," a normal finding in psychophysical studies (i.e., relative hyper- and hypometric responses, respectively, to lower and upper ends of a stimulus range). Additionally, the limits of manual dexterity and highly responsive torque motor driving the rotating chair promoted hypermetric responses at small angles particularly during kinetic-matching strategies, perhaps explaining the larger GBS y intercept value in the sighted in which kinetics were significant contributors to GBS spatial performance (Table 3)].

GBS strategy. Multi-regression analysis of the combined responses (Table 3, labeled blind) for the blind group showed that stimulus angle was the main predictor of response angle.

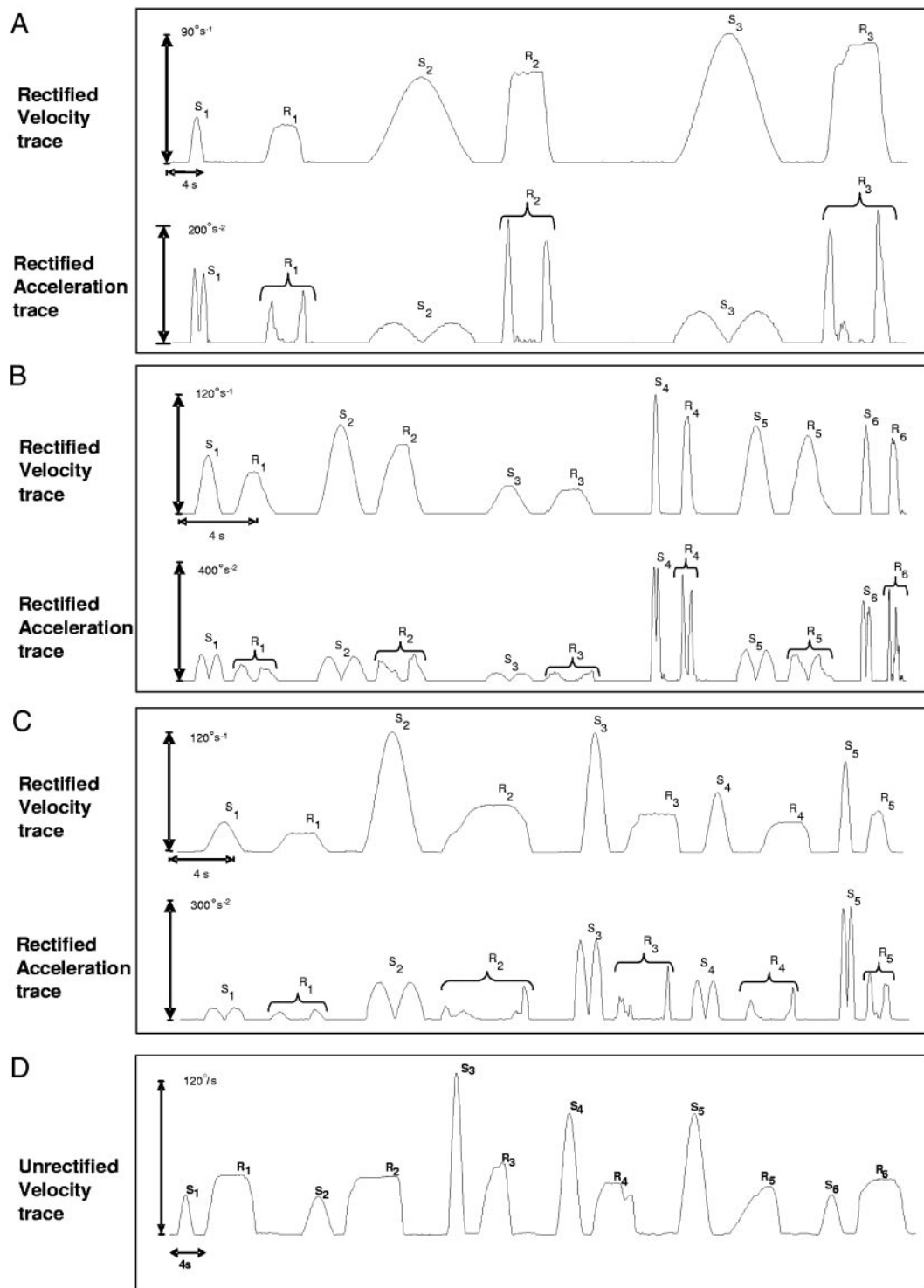


FIG. 4. Representative traces for GBS (A–C) and CTC (D). *Top* and *bottom* traces in each of the panels (A–C) show the velocity (labeled) and acceleration (labeled) profiles respectively of stimulus (S) and response (R) during the GBS task. Traces have been rectified as discussed in Fig. 2. Each acceleration response has been bracketed to ease visual inspection since there are 2 acceleration maxima per velocity maximum. A: this shows S10's strategy, which involved matching the peak velocity but not the peak acceleration. B: responses from S2 where there is matching of velocity and acceleration. C: response strategy of S9. Here the dynamics of the stimulus movement are ignored, and the subject recovers the response displacement. Quantitative analysis of these and other subjects' strategies is given in Table 2 (right). D: unrectified velocity traces for the CTC task from S1. Note these are unrectified traces because in CTC both stimulus and response are in the same direction. All subjects' CTC velocity profiles showed the same form, i.e., there was no correlation between stimulus and response dynamic parameters.

Individual blind subjects' strategies also showed good correspondence between qualitative and quantitative methods of analysis as for the sighted subjects. Individual analyses (Table

2, *bottom third* of table, right-hand side) showed stimulus angle to be the major contributor to response angle for five subjects (median P value <0.01 , range: 0.0001–0.08; see Table 2). In

TABLE 3. Group performance and strategy

Group	Multiple Regression: Predictors of Response Angle (Response Angle vs. Stimulus Angle, Velocity, Duration, Acceleration)					
	Multiregression fit		Angle	Velocity	Duration	Accel.
	<i>n</i>	<i>r</i> ²	β	β	β	β
Sighted	561	0.84	0.75	0.20 ^{ψ}	–	–0.14 ^{τ}
Blind	287	0.74	0.76	–	–	–

This shows the correlation coefficients (*r*²), the standardized slopes (β) and the number of data points per analysis (*n*) for linear and multiple regressions for grouped data. All *r*² and β values have a *P* value < 0.0001 unless otherwise stated (ψ = *P* < 0.05, τ = *P* < 0.01). Nonsignificant values are omitted.

subject B2, stimulus velocity and acceleration significantly predicted response angle (Table 2). GBS strategy did not appear to be related to velocity storage time constants; e.g., B4 and B6 both possessed ultrashort time constants but showed divergent GBS strategies, i.e., B4 used a mixed spatial and kinetic strategy, whereas B6 utilized a spatial strategy (see Table 2; toward bottom on right of table). Overall however, blind subjects utilized a position-based strategy for the GBS task.

GBS encoding of velocity, acceleration, and motion duration. Group analysis showed that response velocity was dependent on stimulus velocity (β = 0.50; *P* < 0.01) and acceleration (β = 0.18; *P* < 0.05), whereas response acceleration, as for the sighted group, was predicted by stimulus acceleration only (β = 0.48; *P* < 0.0001). Group response motion duration was predicted only by stimulus duration (β = 0.47; *P* < 0.0001). The individual results shown in Table 4 confirm that

congenitally blind humans can also encode head angular velocity and acceleration at perceptual level; i.e., perception of primary and derived vestibular signals is not affected by congenital blindness.

LABYRINTHINE-DEFICIENT SUBJECTS. *Displacement and tempo-kinetic matching.* Regressions for the displacement performance of labyrinthine-deficient subjects L1 and L2, respectively, yielded *r*² values of 0.19 and 0.18 (Table 2; bottom). Matching of stimulus kinetics was similarly poor (defined as regression *r*² < 0.5) with stimulus-response regressions giving L1: velocity: *r*² = 0.16; acceleration: *r*² = 0.08; time: *r*² = 0.13 and for L2: velocity: *r*² = 0.14; acceleration: *r*² = 0.32; time: *r*² = 0.06. Thus tactile stimuli did not afford accurate navigation in GBS (compare with normal values for GBS in Table 2) in agreement with previous data with this technique (Brookes et al. 1993; Metcalfe and Gresty 1992).

TABLE 4. Individual kinetic-matching during GBS

Subject	Predictors of Response Peak Velocity During GBS via Multiple Regression Model [Response peak velocity vs. stimulus angle (<i>θ</i>), velocity (<i>v</i>), time (<i>t</i>), acceleration (<i>a</i>)]					Predictors of Response Peak Acceleration During GBS via Multiple Regression Model [Response peak acceleration vs. stimulus angle (<i>θ</i>), velocity (<i>v</i>), time (<i>t</i>), acceleration (<i>a</i>)]					Predictors of Response Motion Duration During GBS via Multiple Regression Model [Response motion duration vs. stimulus angle (<i>θ</i>), velocity (<i>v</i>), time (<i>t</i>), acceleration (<i>a</i>)]				
	Model fit	<i>θ</i>	<i>v</i>	<i>t</i>	<i>a</i>	Model fit	<i>θ</i>	<i>v</i>	<i>t</i>	<i>a</i>	Model fit	<i>θ</i>	<i>v</i>	<i>t</i>	<i>a</i>
	<i>r</i> ²	β	β	β	β	<i>r</i> ²	β	β	β	β	<i>r</i> ²	β	β	β	β
S1						0.72				0.85	0.80			0.34	
S2	0.88		0.80		0.26	0.87				1.23	0.92	–0.69	0.87	0.94	–0.64
S3											0.64			0.60	
S4	0.43		0.74			0.61				0.97	0.81		0.42	0.40	–0.35
S5	0.62			–0.59							0.83	–0.63	0.5	1.20	
S6	0.83		0.76			0.76				1.12	0.72			0.88	
S7	0.85		0.45		0.39	0.91				1.1	0.83	0.50		0.65	–0.33
S8	0.69		0.75			0.68				0.69	0.85				–0.35
S9	0.81	0.61			0.35	0.76				0.74	0.86			0.77	–0.28
S10	0.61		0.99								0.67			0.42	
S11	0.81		0.78			0.82				1.27	0.88			0.82	–0.33
S12	0.71	0.88			0.53	0.59				0.80	0.86		0.56	0.73	–0.41
B1						0.49				0.84	0.68				
B2	0.63		1.1								0.54			0.71	
B3	0.60				0.80	0.80			0.47	1.42	0.63		0.69		–0.75
B4	0.72		0.96			0.78				0.97	0.72			0.71	
B5						0.59				0.44	0.67			0.95	
B6	0.56		0.94			0.59				0.44	0.69	1.07			

Predictors of peak response velocity (left), peak response acceleration (middle) and motion duration response (right) obtained by multiple regression analysis. This shows the correlation coefficients (*r*²), the standardised slopes (β); nonsignificant values (*P* > 0.05) are omitted. Correlations inherent to the stimulus set (e.g., *r*² = 0.25 for stimulus peak velocity vs stimulus peak acceleration) are shown labelled “Inherent correlations”. (large numbers of empty boxes in the middle section, indicates that acceleration response is poorly predicted by other factors except stimulus acceleration). Inherent correlations (*r*²): *v* vs. *a* = 0.25; *v* vs. *t* = 0; *a* vs. *t* = 0.48 (see Table 2 for relevant θ correlations)

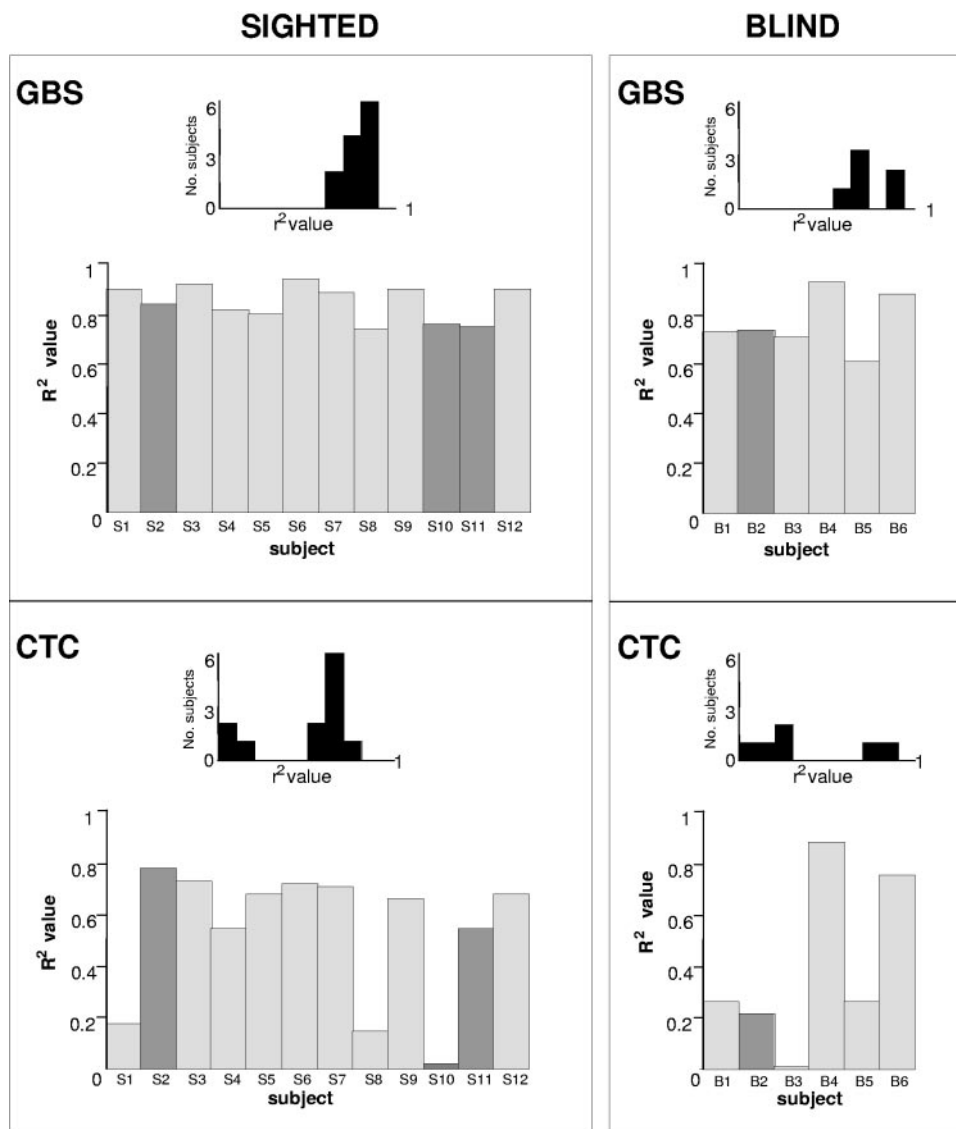


FIG. 5. Bimodal within-group CTC performance. *Smaller top figures* represent frequency distribution plots for the r^2 values of the individual regressions (response angle vs. required angle) reflecting performance for sighted and blind subjects performing GBS and CTC (as labeled). Thus the x axis represents r^2 value and y axis represents number of subjects. Note the bimodal “all-or-none” distributions of performance during CTC. *Larger bar charts*: graphically represent individual performances (r^2 values) obtained from displacement linear regressions (response vs. stimulus angle). Thus the y axis is the r^2 of the stimulus-response displacement linear regressions for sighted ($S1-S12$) and blind ($B1-B6$) subjects for GBS and CTC. Light colored bars identified subjects who utilized a predominantly position-based strategy vs. dark colored bars that identified “kinetic-matching” strategy during GBS (as defined by the predictors of response displacement in Table 2).

Experiment 3: path completion task (CTC)

SIGHTED SUBJECTS. *CTC strategy.* Strategy was uniform with all subjects employing a stepwise velocity response (Figs. 2C and D) with no significant correlation between stimulus peak velocity versus response peak velocity; stimulus peak acceleration versus response peak acceleration and stimulus duration versus response duration for all subjects ($P > 0.05$ for all comparisons). For example, the combined response-stimulus velocity matching for 12 sighted subjects yielded: $r^2 = 0.0009$ and regression slope = -0.12 .

Group CTC displacement performance (response angle vs. required angle). Performance in CTC was assessed by comparing the angle required to complete the circle (S') and the response angle (R') and was described by $R' = 0.72 S' + 88^\circ$ and $r^2 = 0.35$ for all data points from all sighted subjects ($n = 571$). As a group, sighted subjects showed more variability in the CTC as compared with the GBS task (r^2 significantly different; $P < 0.05$, Fisher's r' transformation) although the slopes of the respective regressions were not significantly different ($P > 0.05$). Figure 3 (*top right*) shows the regression

plot between S' and R' for CTC for the average of all response data points for each particular stimulus angle for the sighted group.

In contrast to between-subject GBS performance which was normally distributed within the group, that for CTC was bimodally distributed with two clusters at opposite ends of the performance scale (Fig. 5 sighted CTC). The nine subjects performing CTC well showed similar GBS-CTC performance (GBS: $R = 0.79 S + 33$, $r^2 = 0.75$ vs. CTC: $R' = 0.79 S' + 54$, $r^2 = 0.55$). The three subjects performing CTC poorly (defined as regression $r^2 < 0.5$) showed comparable GBS displacement performance ($R = 0.79 S + 33$, $r^2 = 0.75$) when compared with that of the other nine subjects ($R = 0.75 S + 30$, $r^2 = 0.82$). Thus GBS performance (Table 2) did not appear to reliably predict CTC performance.

BLIND SUBJECTS. *CTC strategy.* As for the sighted group, all blind subjects' responses showed a step-like displacement strategy (of the type shown in Figs. 2C and 4D) with no significant correlation ($P > 0.05$) between stimulus and response kinetics.

Group CTC performance (response angle vs. required angle). When the regression between angle required (S') and response angle (R') of all data points from all blind subjects for CTC was compared with that for the sighted group, blind CTC performance ($R' = 0.58 S' + 112^\circ$ and $r^2 = 0.14$; $n = 287$) was significantly worse ($P < 0.05$) for regression slope (t -test) and r^2 values (Fisher's r' transformation) although regression y intercepts were not significantly different between groups ($P > 0.05$). Figure 3 (bottom right) shows the regression plot between R' and S' for the average of all response data points for each particular stimulus angle for the blind group during CTC. As in the sighted group, blind subjects also showed a bimodal performance distribution (Fig. 5) although the proportion of poor performers was higher viz. 4/6 for the blind versus 3/12 for the sighted (Table 2).

CTC performance and the perceptual vestibular time constant. The two blind subjects with the best CTC performance ($B4$ and $B6$, Table 2) also had the shortest perceptual vestibular time constants (Fig. 1). On initial inspection, this seems counterintuitive because predominantly large angle and thus potentially low-frequency responses, are made in CTC as compared with GBS. However, subjects' responses (including the 2 subjects with ultra-low time constants) in CTC were rarely >6 s (i.e., frequency ≥ 0.1667 Hz) thus relegating the velocity storage to secondary importance in our experiments.

LABYRINTHINE-DEFICIENT SUBJECTS. *CTC displacement performance.* As for GBS, labyrinthine-deficient subjects $L1$ and $L2$ were unable to perform the CTC task. Linear regression between angle required and angle made to complete the circle gave r^2 values for both subjects of 0.05 ($P > 0.05$).

Assessment of within-subject variability for GBS and CTC response performance

Figure 6 shows individual plots of angle made versus angle required for blind subjects $B1$ – $B6$ (as labeled) for GBS (left) and CTC (right). The bold line is the average angle made for each required angle with the upper and lower lines representing the maximum ranges of the subjects' response. Also shown are the 95% confidence intervals (gray) for sighted group performance for GBS and CTC. Note how the individual blind subject performance approximates the normal confidence intervals for GBS but not for CTC (except conspicuously for $B4$ and $B6$), indicating greater within-subject variability for CTC compared with GBS in the blind subjects. To further gauge within-subject variability, a univariate ANOVA of the group regression residuals (see METHODS) was performed and compared sighted GBS, sighted CTC, blind GBS, and blind CTC. The ANOVA showed significant differences between the groups [$F(3,1725) = 115.38$; $P < 0.0001$]. Post hoc testing (Scheffe's test) showed that blind group averaged residuals were 44% larger than the sighted CTC residuals (79.22 vs. 45.50° ; $P < 0.0001$), whereas GBS residuals were not different between sighted and blind (25.84 vs. 21.20° ; $P = 0.67$). The average within-subject variability was larger in CTC than GBS for both groups ($P < 0.0001$). In summary, the overall within-subject variability was not different for GBS between both groups whereas the blind group showed a greater overall within-subject variability during CTC.

Comparison of the accuracy of GBS and CTC response performance for 180° stimuli

While identical stimuli were used for GBS and CTC, the stimulus-response pairings were different between these tasks (e.g., 90° stimulus required responses of 270° for CTC and 90° for GBS) except uniquely for a 180° stimulus because the required response magnitude was 180° for GBS and CTC. Figure 7 shows the results of the sub-analysis for the percentage displacement error for responses to 180° stimuli. If subjects utilize the same mechanism for GBS and CTC, then the 180° performance should be the same for both tasks.

SIGHTED. The mean percentage error displacement response to 180° stimuli was significantly different between GBS and CTC tasks for the sighted group (Fig. 7, top; $P < 0.0001$; paired t -test). The mean percentage errors were still significantly greater for CTC (62.6 vs. 29.5%; $P < 0.0001$; $n = 54$; paired t -test) when poor CTC performers (defined as regression $r^2 < 0.5$) were removed from analysis or when analysis was confined to those sighted subjects exclusively using a spatial GBS strategy i.e., $S5$, $S6$, $S9$ (GBS = 13.6%, CTC = 28.6%; $P = 0.03$; $n = 18$; paired t -test). Thus navigational performance for 180° stimuli was worse for CTC versus GBS "modes" of navigation.

BLIND. A comparison between CTC and GBS responses to 180° stimuli (Fig. 7, bottom) showed significantly worse CTC performance ($P < 0.001$; paired 2-tailed t -test).

Thus the results from the 180° analysis show a clearly different 180° performance between GBS and CTC indicating that subjects utilize different navigational modes during GBS compared with CTC.

DISCUSSION

The aims of this study were to investigate the impact of early visual loss on vestibular perception in relation to the perceptual velocity storage mechanism and the use of vestibular signals in angular motion perception and navigation.

Perceptual vestibular time constant

Using a perceptual method, we found that vestibular time constants are shortened by 50% in the congenitally blind, indicating deficient velocity storage. Eye-movement methods of estimating the vestibular velocity storage time constant in the visually impaired may be complicated by oculomotor time constant abnormalities. This could partially explain the finding of ultra-short vestibular time constants (1–2 s) reported in congenital nystagmus and late-onset blind subjects (Demer and Zee 1984; Sherman and Keller 1986). Using a perceptual method to circumvent this issue in congenital nystagmus, Okada et al. (1999) found a vestibular time constant of 7 s. Additionally, assessing the velocity storage mechanism via the VOR is not feasible in the congenitally blind as they lack coordinated eye movements (Kompf and Piper 1987; Sherman and Keller 1986).

Our perceptual finding of a deficient velocity storage in congenital blindness is in agreement with animal data (Harris and Cynader 1981; Tusa et al. 2001). An adaptive shortening of the velocity storage time constant, as shown to occur in healthy

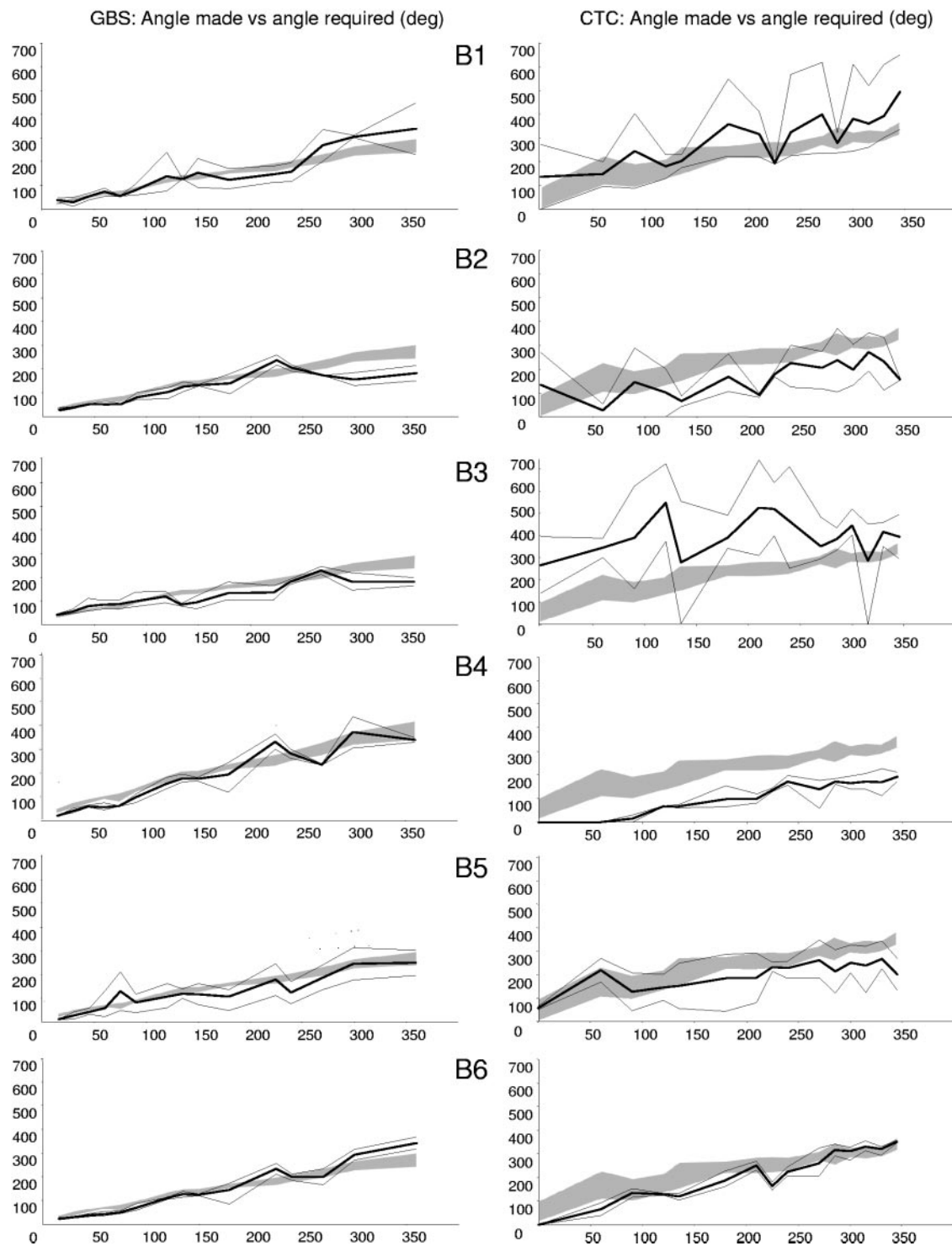


FIG. 6. Comparing Blind individual CTC and GBS performance to the sighted group. Blind subjects' individual performances, plotted as black lines (average angle made $\pm$ maximum and minimum response vs. required angle), compared with the normals group response shown in gray (group average $\pm$ 95% confidence intervals).

sighted subjects in response to motion sickness-inducing stimuli (Cohen et al. 2003; Grunfeld et al. 2000), could explain short perceptual time constants in the blind. However, the blind are not particularly exposed to motion sickness stimuli and show equivalent motion sickness susceptibility to the sighted (Graybiel 1970). A more likely explanation for our findings is the failure of the development of the velocity storage mechanism due to early visual loss in agreement with animal (Harris

and Cynader 1981; Tusa et al. 2001) and neonate data (Weissman et al. 1986). Interestingly subjects with degraded visual motion input, such as those with congenital nystagmus and acquired external ophthalmoplegia, also show a short perceptual vestibular time constant (Faldon et al. 1997; Grunfeld et al. 2003; Okada et al. 1999). Therefore our current data and previous findings suggest that vision continuously recalibrates the vestibular system; in the absence of vision, or in the face of

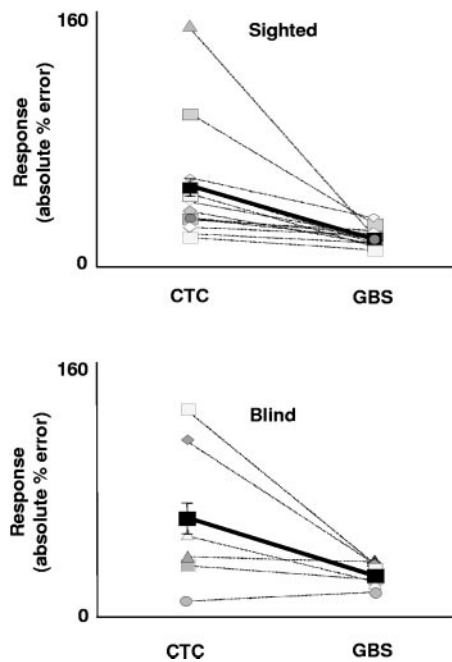


FIG. 7. Percentage error of displacement responses for 180° stimuli for CTC and GBS. *Top*: percentage error of response for sighted subjects. *Bottom*: percentage error of response for blind subjects. Note that percentage error responses for 180° stimuli were significantly larger ($P < 0.05$) for CTC vs. GBS tasks for both groups shown. Each broken line links the CTC and GBS % error responses for 180° stimuli for each individual. The thick black line links the group average of the displayed individuals for CTC and GBS % error responses for 180° stimuli.

prolonged visuo-vestibular mismatch, the vestibular time constant drops progressively to a 4- to 7-s default value.

VESTIBULAR NAVIGATION. *Path reproduction.* Our findings indicate that angular path reproduction (i.e., GBS) under vestibular guidance can be successfully performed via multifarious strategies including the use of spatial, kinetic, and temporal parameters either independently or in combination. Importantly, the labyrinthine deficient patient results exclude any significant somatosensory contribution in this task (Brookes et al. 1993; Metcalfe and Gresty 1992). The exclusive use of motion dynamics during GBS is exemplified by sighted subjects S2, S10, and S11, who ignored rotational displacement and simply matched kinetics. We also report the first psychophysical data showing that angular acceleration, distinct from somatosensory force perception, or indeed angular velocity perception, is not only encoded at perceptual level but is also utilized in angular vestibular navigation (Table 4 and Fig. 4B). This finding is supported by animal data showing the encoding of angular acceleration at the single cell level in the cerebral cortex (Klam and Graf 2003). Blind and sighted path reproduction group displacement performances were equivalent. Both sighted and blind groups mostly utilized spatial parameters in performing GBS although the sighted group also matched kinetic parameters to a modest degree (Table 3). Individual analysis also showed that sighted and blind subjects were able to perceive and match stimulus displacement as well as stimulus dynamics (Table 4) viz. velocity, acceleration and motion duration. These findings indicate that some aspects of vestibular perception are entirely independent of visual mechanisms, despite the observed influence of vision on velocity

storage (see above) and the acknowledged role of vision in continuously recalibrating vestibular processing (Gonshor and Jones 1973).

Path completion. Navigation paradigms, as does everyday navigation, frequently involve the calculation of a trajectory that then has to be followed under some form of sensory control; the CTC is simply a rotational form of such a task. Specifically, CTC, unlike GBS, cannot be performed by a reproduction of stimulus angle or kinetics and was thus developed to assess true spatial re-orientation. In this regard, CTC and GBS are respectively analogous to the inferential and route navigation tasks developed in locomotor studies (Thinu-Blanc and Gaunet 1997; Loomis et al. 2001). In contrast to GBS, CTC can only be performed with an accurate positional signal and the requisite mental computations.

We found that subjects, irrespective of visual experience, were less accurate and more variable at CTC than GBS. A possible explanation is that the spatial navigation mechanism used for guiding angular orientation is calibrated using inputs occurring during everyday life. Calibration of such a mechanism would occur primarily with GBS-type tasks, e.g., turning away from a starting point and back to it, with the goal to achieve good average accuracy for the most common turning angles. Another explanation for the lower GBS-performance variability could be the amount of information available to guide the inbound, response leg. Thus in GBS, a combination of kinetic matching and an on-line estimation of position, as found in normal subjects in this study, may allow for less variability than in CTC in which only displacement guides response.

Because vestibular input is essential for navigation during locomotor turning in the dark in sighted subjects (Glasauer et al. 2002), comparison of our results with the locomotor literature is warranted. First our GBS findings indicate that the early blind also possess a functionally useful vestibular signal for locomotor turns. Second, comparison of sighted versus blind performance in CTC and GBS parallel those of the locomotor literature (Gaunet and Thinu-Blanc 1997); i.e., equivalent path reproduction (here GBS) versus worse blind group inferential task navigation (here CTC). Ungar (2000) suggested that worse blind performance during inferential tasks reflected inter-individual performance variability rather than a true deficit because some blind individuals were able to attain sighted subjects' performance. Again this pattern is reflected in our results, because B4 and B6 displayed superior CTC performance. Thus our vestibular navigation findings appear to closely match those from the blind locomotor literature and suggest that a deficit in the vestibular navigation component of locomotion (i.e., turning without vision) may explain some blind individuals' worse inferential locomotor navigation.

Is the relative spatial deficit observed in the blind group during CTC a general spatial deficit or is it specific to vestibular navigation and/or locomotion? Several studies have found that overall, the early blind show a spatial deficit when engaged in more complex, inferential, spatial tasks (e.g., CTC), from mental rotation to locomotor tasks (Hill et al. 1993; Loomis et al. 2001; Thinu-Blanc and Gaunet 1997; Ungar et al. 1995, 1996, 1997a,b). One explanation for this general spatial deficit could be the reduced spatial working memory capacity reported in the congenitally blind (Cornoldi et al. 1991). Indeed

vestibular navigation is impaired under conditions of increased cognitive load (Glasauer et al. 2006; Yardley et al. 1999), and the increased working memory demands of CTC (compared with GBS), could explain worse CTC performance in the blind. Interestingly, the functional integrity of the hippocampus, a key region in spatial (particularly allocentric) cognition, is reliant on intact vestibular function but not early visual input (Brandt et al. 2005; Russell et al. 2006; Save et al. 1998). Despite this, in early blind animals, sufficient spatially directed physical activity is required for the adequate functioning of hippocampal spatial systems (Save et al. 1998). This observation could explain why spatial deficits in blind individuals were associated with use of poor (nonallocentric) spatial strategies but that physical training could improve performance in tandem with the use of a more allocentric-based navigation (Ungar et al. 1997b). It is also consistent with the suggestion that superior locomotor navigation may be related to past experience (Loomis et al. 2001; Thinus-Blanc and Gaunet 1997). Thus although the blind may display a general, mainly allocentric spatial deficit, such deficits may result from the use of less efficient strategies, potentially related to previous experience.

Interindividual variability in the congenitally blind

Two blind subjects, *B4* and *B6*, displayed ultra-short vestibulo-perceptual time constants as well as superior CTC performance during navigation. These two subjects were also the higher scorers in the lifetime physical activity scale. It is therefore tempting to speculate that these three aspects may be inter-related. Superior CTC performance could be related to ultrashort perceptual time constants of 2–3 s (Table 1) because this would attenuate potentially disorienting postrotational sensations. Although ultrashort time constants could represent a pure cupula output (estimates of the cupula time constant range from 4 to 7 s) (Büttner and Waespe 1981; Dai et al. 1999; Gizzi and Harper 2003), an alternative view is that they may be due to an active neural high pass filtering of the canal velocity output as postulated by Baloh et al. (1988). Such a central high pass filter would further suppress potentially erroneous vestibular signal drifts with concomitant improved locomotor and vestibular navigation. Why ultrashort time constants should develop in *B4* and *B6* is unclear, but one explanation is that this phenomenon is a form of activity-dependent habituation of the vestibular signal (Jager and Henn 1981; Loomis et al. 2001; Osterhammel et al. 1968; Thinus-Blanc and Gaunet 1997; Ungar et al. 1995, 1997b). Alternatively, inherently shorter vestibular time constants in some subjects could have promoted their predilection to physical activity, but the available evidence indicates that activity shortens vestibular time constants (Grunfeld et al. 2000; Jager and Henn 1981; Osterhammel et al. 1968) not the other way round. Whatever the relationship between physical activity and the perceptual vestibular time constant, it is likely that cerebellar mechanisms, with their prominent roles in vestibular processing, motor control, and neural plasticity (Ungerleider et al. 2002), must have played a part. It is interesting that early blind humans display abnormal GABA binding specifically in the cerebellum but not cerebral cortex (Mishina et al. 2003; Sanabria-Bohorquez et al. 2001) because activity-dependent habituation of vestibular mechanisms may be mediated by cholinergic and/or GABA activation of cerebellar structures (Solomon and Cohen 1994; Tan et al. 1993). Another possibility for *B4* and *B6*'s

superior CTC performance could be directly related to their past physical activity (i.e., not specifically related to shortened vestibular time constants), which may promote the development of superior navigational strategies as discussed in the preceding section. Thus although our observations are based on only two subjects, thereby precluding strong conclusions, our findings support the promotion of physical activity in blind subjects as an aid to improved navigational skills.

Conclusion

The perceptual vestibular velocity storage mechanism is deficient in subjects with early visual loss suggesting that vision is important for its normal development. An alternative explanation would be that velocity storage develops normally, but in the absence of vision, it is modified or suppressed. Some congenitally blind subjects possess ultra-short perceptual vestibular time constants (2–3 s), which may reflect either a pure cupula response or an active neural suppression of low-frequency, potentially disorienting head-velocity signals. Visual mechanisms are not required for the perception of vestibular signals, but visual experience may facilitate the ability to manipulate vestibularly derived angular space during angular path completion tasks. Our results suggest that the brain uses multiple modes of information processing such as spatial and kinetic-based navigation. We speculate that CTC-type tasks may be more reliant on spatial cognitive mechanisms, e.g., spatial working memory, which is relatively impaired in the congenitally blind thus explaining the increased variability in response in this group during CTC. The observed association between superior vestibular navigation and ultra-short perceptual vestibular time constants in the blind could be linked by a co-factor of extensive previous physical activity. This possibility suggests that long-term physical activity in congenitally blind subjects may improve navigational performance and thus could have implications for the long-term orientation and mobility training of such subjects.

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