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Gaze direction affects linear self-motion heading discrimination in humans

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Abstract

We investigated the effect of eye-in-head and head-on-trunk direction on heading discrimination. Participants were passively translated in darkness along linear trajectories in the horizontal plane deviating 2° or 5° to the right or left of straight-ahead as defined by the subject's trunk. Participants had to report whether the experienced translation was to the right or left of the trunk straight-ahead.

In a first set of experiments, the head was centered on the trunk and fixation lights directed the eyes 16° either left or right. Although eye position was not correlated with the direction of translation, rightward reports were more frequent when looking right than when looking left, a shift of the point of subjective equivalence in the direction opposite to eye direction (2 of the 38 participants showed the opposite effect).

In a second experiment, subjects had to judge the same trunk-referenced trajectories with head-on-trunk deviated 16° left. Comparison with the performance in the head-centered paradigms showed an effect of the head in the same direction as the effect of eye eccentricity.

These results can be qualitatively described by biases reflecting statistical regularities present in human behaviors such as the alignment of gaze and path, and combined head and eye contributions to eccentric gaze. Given the known effects of gaze on auditory localization and perception of straight ahead, we also expect contributions from a general influence of gaze on the head-to-trunk reference frame transformations needed to bring motion related information from the head-centered otoliths into a trunk-referenced representation.

Keywords: vestibular, otoliths, linear heading, perception, human, eye, neck

Introduction

During navigation, humans and animals maintain a representation of heading, the direction of self-motion, which is computed from the integration of multimodal sensory cues from the visual, acoustic, vestibular and tactile sensory organs (Britten, 2008). Optic flow provides heading cues from radial patterns of observed relative scene motion in a retino-centric reference frame (Lappe et al., 1999; Macuga et al., 2006); acceleration signals from vestibular organs provide a head-centric inertial self-motion signal (Angelaki and Cullen, 2008), while efference copies of motor commands and proprioceptive signals from the neck and the trunk complement the visual and vestibular systems in the processing of heading information (Crowell et al., 1998; Warren, 1998).

Congruent multisensory information can be integrated to generate better estimates (Stein & Stanford, 2008), but, since different sensory modalities work in different reference frames, it can also lead to systematic errors related to the reference frame transformations (Schlicht & Schrater, 2007). Enhanced performance in heading perception is observed when visual and vestibular information are congruent, and there is evidence that visual and vestibular cues are combined optimally; with relative weights reflecting their relative precision (Fetsch et al. 2009), at least as long as the two inputs are congruent enough to be considered as coming from a single source (Koerding et al., 2007; Butler et al., 2010). In those experiments retinal, head and trunk-based reference frames aligned and the effect of misalignment due to deviations of eye-in-head and head-on-trunk on heading perception is not known. However, eye position affects the localization of acoustic targets (Lewald, 1997; Razavi et al., 2007; Van Barneveld and Van Opstal, 2010), leads to pointing errors (Lewald & Ehrenstein, 2000a) and shifts the perception of straight ahead (Cui et al., 2010). Head on trunk eccentricity leads to similar effects on sound lateralization (Lewald & Ehrenstein, 1998; Lewald et al., 2000b). It is therefore necessary to study whether these factors also affect heading perception.

Here we investigated how eye-in-head and head-on-trunk direction affect heading perception during inertial motion. Humans and monkeys can use inertial information to discriminate the direction of motion (Gu et al., 2007, MacNeilage et al. 2010) and precision in this task likely depends on intact otolith organs (Valko et al., 2012), the linear accelerometers of the vestibular periphery. We studied the effect of eye and head deviation in healthy human subjects. They were passively translated in the dark along linear horizontal trajectories and were asked to report whether the translation had been right or left with respect to the trunk straight-ahead. A first experiment looked at the effect of eye direction; subjects performed the two alternative forced-choice task with centered head-on-trunk but with eye-in-head deviated 16° to the right or left. In different versions of the experiment eccentric gaze was maintained either with or without a small visual target (**LED OFF paradigm**), and eye deviation was maintained transiently (**alternating fixations paradigm**) or for long stretches of time (**sustained fixations paradigm**). The results were similar across manipulations, which suggests that the main effect was due to the direction of eye-in-head and independent of visual input. A second experiment assessed heading discrimination with head-on-trunk deviated to the left and eye-in-head either centered or to the right (**eccentric head-on-trunk paradigm**). Comparison with the results of the first experiment (centered head-on-trunk) suggests that head-on-trunk also affects heading discrimination.

In the discussion we explore how regularities in natural behavior could influence perception of heading. In particular we consider that i) normally both eye and head contribute to head-free gaze shifts and ii) eye head and trunk align during natural locomotion and implement them as priors in a simple Bayesian framework. Bayesian inference provides a mathematical framework to study top-down effects, which include prior knowledge about the relative frequency of a stimulus in the natural environment but also other contextual effects (Colas et al., 2010). It is consistent with the view that perception is a creative process in which bottom-up sensory information is combined with top-down contextual information (Meyer, 2011; Bastos et al., 2012) and has been extensively used to describe both multisensory integration and systematic biases due to incorporation of prior knowledge in many perceptual tasks (Ernst & Banks, 2002; Weiss et al., 2002; Laurens & Droulez, 2007; Fetsch et al., 2009).

Materials and methods

Participants

38 healthy volunteers participated in the head centric tasks and 17 in the head eccentric task (age 20 – 50 years old). Subjects gave their written consent to participate in this experiment after being informed of the experimental procedure. This study was compatible with Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki) and was approved by the local ethics committee. Except for the authors, participants were unaware of the purpose of the study.

Apparatus

To deliver the motion stimuli, we used a six degree of freedom motion platform (E-Cue 624-1800 motion system, built by FCS Simulator Systems, Schiphol, Netherlands). Subjects sat in a chair mounted on the platform. An individually molded thermoplastic mask (Sinmed, Netherlands) immobilized the subjects' head, making sure that the head moved with the motion platform. A four-point safety belt with straps over the shoulders and hips secured the body to the platform. A box with two push buttons was attached on a safety bar in front of the subject and served as the reporting device.

Data acquisition was controlled with LabVIEW (National Instruments, U.S.A.) with a sample frequency of 1000 Hz. Data included the position of the platform as well as the voltage associated with the two report buttons.

Three small light emitting diodes (LEDs) were mounted on the platform approximately 140 cm in front of the subject. They served as fixation targets to direct the gaze of the participants. The center LED was positioned straight ahead from the subject's trunk. The left and right LEDs subtended a visual angle of 16 degrees with respect to straight-ahead (Figure 1).

In three recordings we recorded the position of the left eye with a video-oculography system (EYESEECAM, Munich, Germany).

Experimental Protocol

Subjects were passively translated in complete darkness except for the light-emitting diodes (LEDs) that guided the subject's gaze. We used a one-interval, two-alternative forced choice (2AFC) task in which participants had to judge whether they had moved toward the right or left relative to their trunk's straight ahead. Translations were linear trajectories in the horizontal plane deviating 2 or 5 degrees left or right relative to the subject's trunk straight-ahead. The translations of the motion platform were the same in all paradigms and therefore were stable when referred to the trunk.

Paradigms differed only in viewing conditions and head orientation. The otolith organs were stimulated about the midline in head centric paradigms and diagonally in head eccentric paradigms.

The beginning of each trial was signaled with a brief sound 2 seconds before motion onset. At this time, one of the LEDs was illuminated as a visual fixation cue. In most of the paradigms the LED stayed on during platform motion and subjects were instructed to maintain fixation throughout the movement. In one paradigm the LED was turned off immediately before motion onset, but participants had to keep their eyes eccentric. After the displacement (duration 1.5s), the platform remained stationary for three seconds and subjects had to report their perceived direction of motion by pressing either the right or left button. The platform moved back to the starting position with the same motion profile as the outward motion and a new trial began.

The volunteers had to complete four blocks with 40 trials in each block (about 6 min per block). Data was collected in a single experimental session. Each experimental paradigm combined the four translation directions with two or three eye positions. The goal was to compare the psychometric curves obtained with different eye or head orientations. The four deviations were presented in pseudo-random order but each block had all conditions presented the same number of times. Details about the stimuli presented in each block varied with the paradigm and are explained below.

The stimulus velocity profile was that of a raised cosine; the total displacement was 0.4 meters and the duration 1.5 seconds. The peak velocity and peak acceleration were 0.53 m/s and 1.38 m/s^2, respectively.

In the following we will describe the position of the LED by its deviation with respect to the trunk (G values in the panels of Figure 1). Since the trunk did not change orientation in space, gaze (the direction of the line of sight in space) coincided with the direction of the line of sight in a trunk-based reference frame. We will use the letter E to denote eye-in-head, H to denote head-on-trunk and G, to denote gaze. Under our conditions, G = H+E.

Paradigms with head straight-ahead

In these paradigms, four in total, the head was aligned with the trunk straight-ahead direction (H = 0°). The basic paradigm (A) consisted in fixations which alternated in pseudorandom order between right and left gaze, and were maintained by fixating a visible light emitting diode (LED) which stayed on during motion. Manipulations on this basic paradigm explored the influence of visual feedback (paradigm B) and the duration of eccentric fixation (paradigm C). Another paradigm (D) presented three gaze directions (left, center, right) to assess whether deviation of gaze would also affect precision. There were 46 valid recordings with head straight-ahead corresponding to 38 different subjects (6 subjects participated in more than one paradigm). There were two subjects that did not follow the instructions and whose data was discarded, one in paradigm B and another in paradigm C. The number of participants in each paradigm is given in parentheses.

Paradigm A, Alternating Fixations (N=13): Before and during motion subjects were instructed to maintain an eccentric eye position by fixating the left or right LED (E = -16° or 16°). Within each block the order of right/left LED presentations alternated randomly. At the end of the displacement, the eccentric LED was extinguished and the center LED switched on. Subjects were instructed to look at the center LED when it appeared. The paradigm consisted of 8 conditions (4 trajectory deviations × 2 eccentric eye positions). Each block contained 5 presentations of each condition and the whole experimental session provided 20 repetitions per condition.

Paradigm B, LED OFF (N=8): Same as paradigm A, except that the LED was turned off just before motion onset. Subjects were instructed to maintain the eccentric eye position during motion. There were 20 repetitions of the 8 conditions (4 trajectory deviations × 2 eccentric eye positions). To examine the residual eye movements during motion, the left eye of three subjects was monitored with the video-oculography system. Smooth eye movements after the guiding LED disappeared were smaller than 1°.

Paradigm C, Sustained Fixations (N=12): A single LED was constantly on for the duration of a block and subjects were instructed to not break fixation of the LED during this time. (1th & 3th block: left LED on, 2rd & 4th block: right LED on or vice versa). There were 20 repetitions of the 8 conditions (4 trajectory deviations × 2 eccentric eye positions).

Paradigm D, 3 LEDs (N=15): Of the four blocks of trials, two were exactly as in paradigm A, with fixations alternating randomly between left and right. In the other two blocks of trials, instead of an eccentric LED, the center LED was on in all trials. There were ten repetitions for each of the 8 conditions with eccentric fixations (4 trajectory deviations × 2 eccentric eye positions) and 20 repetitions of the four conditions with centric fixation (4 trajectory deviations × 1 eye position).

Paradigm with head-on-trunk eccentric

17 subjects completed this paradigm. The mask fixating the participant's head to the back of the seat was made with the participant's head deviating 16 degrees to the left from the trunk straight ahead (H= -16°, Figure 1) so that the head faced the left LED. A laser pointer at the level of the chin indicated when the head was facing the left LED. Trajectories were the same as in the head-centered paradigms, thus they were the same with respect to the trunk, but not with respect to the otoliths. The task remained the same: to report whether the trajectory was felt to the right or the left with respect to the trunk. During motion one of two LEDs was on, one facing the head so that it was fixated with eyes centered in the orbit (E = 0°, G = -16°), the other facing the trunk so that it required an eccentric eye in the orbit (E = 16°, G = 0°). The order of presentation of trajectory deviations and eye positions was randomized. There were 20 repetitions for each of the 8 conditions (4 trajectory deviations × 2 eye positions) giving a total of 160 trials that were divided in 4 blocks of 40 trials each. After the first two blocks the head was freed for a minimum of five minutes before resuming the experiment and completing the last two blocks.

Data Analysis

Data were analyzed offline with customized scripts written in MATLAB (R2007b,The MathWorks, USA). For each recording, trials were sorted according to platform trajectory and LED direction, then the report of the participant was determined, this could be right, left or void if the subject failed to report during a given trial. Overall missed trials were rare but a few subjects did miss a considerable number of them as reported in the Results section. The calculations described below were performed taking into account the actual number of valid trials per condition.

Psychometric Curves

The analysis was based on the psychometric curves, which represent the proportion of rightward responses as a function of trajectory deviation $P_R(\theta)$ (Wichman & Hill, 2001). We calculated a separate psychometric curve for each viewing condition in each experiment (three in the case of paradigm D).

We used two approaches to characterize the psychometric curves; parametric and non-parametric. The parametric approach was based on fitting the data with a cumulative Gaussian function as will be described below. Since the parametric approach could not be applied reliably to participants with low performance, we also defined non-parametric measures to characterize the psychometric curves.

Parametric measures

Assuming that for a given direction of motion (θ) there is a certain probability $p(\theta)$ of rightward responses, the random variable n, which describes the number of right reports in N trials, follows a binomial distribution $n \sim B(N, p(\theta))$. What we measure is the percentage of rightward reports $P_R(\theta)=n(N,p(\theta))/N$. The psychometric curves were parameterized by fitting the underlying probability $p(\theta)$ with a cumulative Gaussian (Klein, 2001):

$$p(\theta; PSE, \sigma) \equiv \frac{1}{\sqrt{2\pi\sigma^2}} \int_0^\infty exp\left[-\frac{\left(\hat{\theta} - (\theta - PSE)\right)^2}{2\sigma^2}\right] d\hat{\theta} \qquad (1)$$

where θ is the trajectory deviation **((-5 -2 2 5)° in all paradigms, independent of head-on-trunk or eye-in-head deviation)** , PSE the point of subjective equality, and σ the psychophysical threshold. PSE and σ were estimated by maximum-likelihood estimation (MLE). The likelihood associated with a given psychometric curve is:

$$L = \prod_k \frac{N!}{n_k!\,(N-n_k)!} p(\theta_k; PSE, \sigma)^{n_k} \left(1 - p(\theta_k; PSE, \sigma)\right)^{(N-n_k)} \qquad (2)$$

In this expression $n_k = NP_R(\theta_k)$ is given by the data and $p(\theta_k)$ by Equation 1. The estimates for PSE and σ minimize the above expression given the data.

To analyze the reports from the paradigm with 3 LEDs we performed an additional fitting procedure in which we explicitly considered PSE as a function of eye position and some random individual bias. The goal was to give an estimate of the 'weight' of eye position. For each participant we fit the whole data set corresponding to the three LEDs with a single set of parameters by considering the following alternative to Equation 1:

$$p(\theta, E; a, b, \sigma) \equiv \frac{1}{\sqrt{2\pi\sigma^2}} \int_0^\infty exp\left[-\frac{\left(\hat{\theta} - (\theta + aE + b)\right)^2}{2\sigma^2}\right] d\hat{\theta} \qquad (3)$$

***E* stands for eye deviation; *a* and *b* are fitting parameters representing the weight and individual bias respectively.** As before, we find the parameters **(*a*, *b*, and *σ*)** that maximize Equation 2, which in this case includes all the twelve data points (3 eye positions × 4 trajectory deviations).

Non-parametric measures

Some psychometric curves were too flat to obtain meaningful fits to a cumulative Gaussian. A psychometric curve was deemed too flat if the percentage correct (PC) was not above chance level.

$$PC = \frac{1}{2} + \frac{1}{4}(P_R(\theta = 2) + P_R(\theta = 5) - P_R(\theta = -2) - P_R(\theta = -5)) \qquad (4)$$

To characterize such curves we defined the bias, B, as the total proportion of rightward responses, so that B can only have values between 0 and 1. When B = 0.5, there is no preference of rightward over leftward reports.

$$B = \left(P_R(5) + P_R(2) + P_R(-2) + P_R(-5)\right)/4 \tag{5}$$

As a measure of sensitivity S we used the difference between the mean proportion of rightward reports for rightwards and leftwards trajectories:

$$s = (P_R(5) + P_R(2) - P_R(-2) - P_R(-5)/2 \tag{6}$$

This quantity is linearly related to the percentage correct measure defined above ($PC = (1+S)/2$).

Parametric versus Non-parametric

Quantities describing the psychometric functions were calculated separately for each subject and each viewing condition. **Only subjects with reliable parametric measures for all psychometric curves were included in analyses involving *PSE* and σ. Thus, either all psychometric curves in a dataset would contribute to both *PSE* and σ, or none of the psychometric curves would. Otherwise, all valid recordings contributed to the nonparametric measures (bias and sensitivity).**

While *PSE* and σ are based on a cumulative Gaussian, non-parametric measures do not make any assumption about the form of the underlying psychometric function and describe 'local' properties of the psychometric curve at the sampled range of trajectory-in-trunk deviations θ = (-5, -2, 2, 5)°. In the case of a cumulative Gaussian psychometric function the two sets of parameters are nonlinearly related by equations (1) (5) and (6), and when *PSE* remains close to zero within the sampled range of trajectory deviations, there is a strong negative correlation between bias and PSE on the one hand, and sensitivity and σ on the other.

The two approaches, although not strictly equivalent, can be viewed as complementary; while the parametric representation provides a direct interpretation and is easier to compare with results in the literature; the non-parametric representation allowed us to use all datasets and was particularly useful in adding power when comparing performance across paradigms.

Statistical analysis

We established whether performance was above chance level for each psychometric curve separately. We considered percentage correct (defined in Equation 4) as the statistic of interest and estimated the distribution of this statistic under the null hypothesis that the psychometric curve $P_R(\theta)$ was constant, that is: $P_R(-5) = P_R(-2) = P_R(2) = P_R(5) = P_{null}$ (where P_{null} corresponds to the best maximum likelihood estimate to the data assuming a constant value for all deviations). We generated the distribution corresponding to the null hypothesis empirically by generating 2000 random draws (each random draw generates a synthetic psychometric curve) from the binomial distribution $B(N, P_{null})$(with N the number of valid trials for each direction of motion for each subject. From this synthetic data we calculated the corresponding percentage correct by using Equation 4 (obtaining 2000 percentage correct values, one for each synthetic psychometric curve derived from the null hypothesis). Percentage correct of the actual measured psychometric curve was deemed above chance level if it lied outside the 95 percentile of percentage correct values derived from the null hypothesis.

We followed a similar procedure to determine whether two psychometric curves from the same subject (each corresponding to a gaze direction) were significantly different. In this case we used as statistic ΔN_R, the difference in the total number of rightward reports for the two curves ($\Delta N_R=4\Delta B$ with B defined in equation 5). We asked whether this value was consistent with the null hypothesis that there was no difference introduced by gaze direction. We calculated the psychometric function corresponding to the null hypothesis pooling all the trials independently of viewing condition $P_{R,null}(\theta) \equiv (P_{R,GAZE\ 1}(\theta)+ P_{R,GAZE\ 2}(\theta))/2$. We used the binomial distribution to empirically generate the distribution of ΔN_0 expected from such $P_{R,null}(\theta)$ values (10000 draws). The two curves were deemed statistically different if ΔN_R lied outside the 95 percentile of ΔN_0.

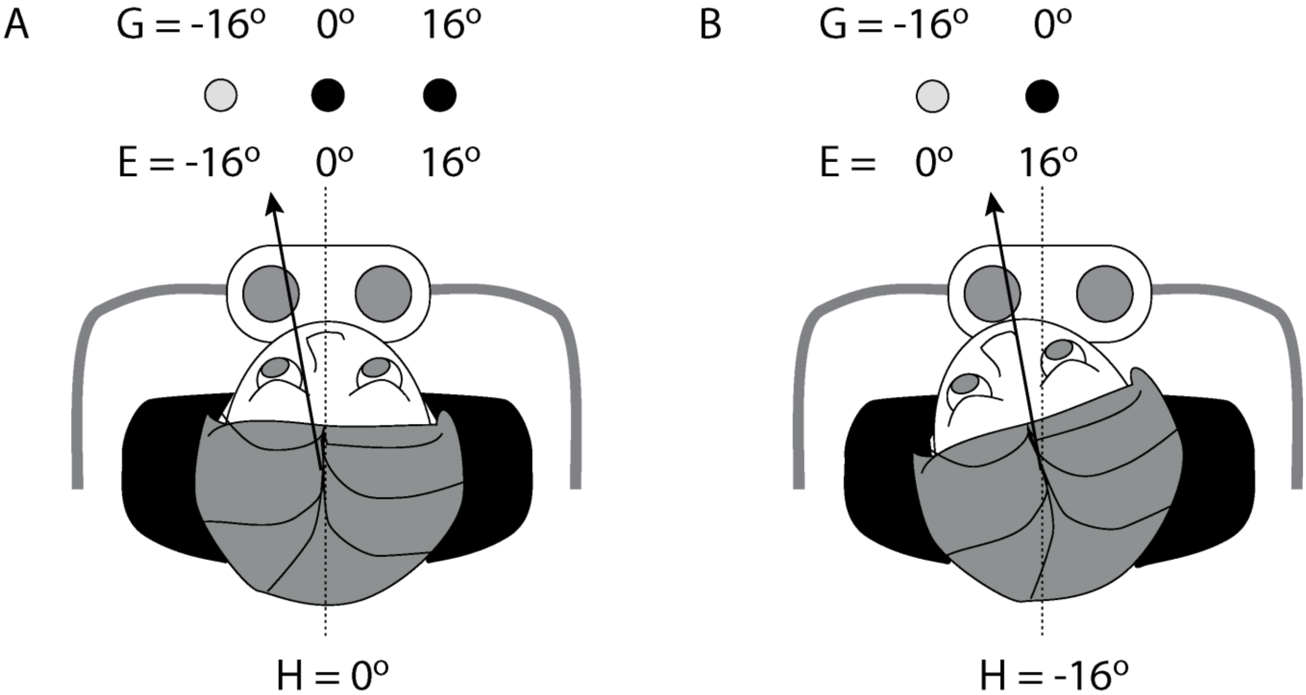

Figure 1 Experimental setup. Paradigms had subjects with head either oriented along the trunk (A) or facing the left LED (B), which deviated 16 degrees from straight ahead (left panel). In all paradigms the actual direction of motion, represented in the diagrams by an arrow, was defined in relation to the trunk straight-ahead (there were four different trajectory deviations symmetric about the trunk straight-ahead). LEDs were mounted on the front railing of the motion platform. The drawings illustrate the situation in which the left LED is on and the participant fixates it either with eye-in-head eccentricity (left panel) or head-on-trunk eccentricity (right panel). H: head-on-trunk, E: eye-in-head, G = H+E, gaze.

Results

The effect of eye-in-head direction

With head centered on the trunk, three paradigms assessed the effect of eye-in-head direction (right vs. left, E = ±16°) on the point of subjective equivalence (*PSE*), and the fourth, which also included E = 0° trials, looked at the influence on precision by comparing σ in trials with E = ±16° and in trials with E = 0°.

There were a total of 46 valid recordings (13 in paradigm A, 7 in B, 11 in C and 15 in D), corresponding to 38 different subjects (6 subjects participated in more than one paradigm). Sometimes participants failed to give a report (missed trial). From the total of 46 valid recordings, 33 had no missed trials and 8 had one missed trial. The number of missed trials in

the remaining 5 recordings was (8, 10, 13, 22 and 33) respectively. In all the expressions including the number of trials per condition *(N)*, only the actual number of valid trials was used.

Most participants showed a significant modulation of reports with the direction of motion. This was assessed by looking at whether percentage correct was significantly different from chance for all psychometric curves belonging to the same subject. Figure 2 shows two sample pairs of psychometric curves, including an example of performance not above chance level (right panel, curve for E = 16°). Significant modulation with direction was found in 10/13 (paradigm A), 7/7 (paradigm B), 7/11 (paradigm C) and 14/15 (paradigm D). If a dataset contained a psychometric curve not above chance level, the whole dataset only contributed to the nonparametric measures (bias and sensitivity) and not to the parametric ones (PSE and σ).

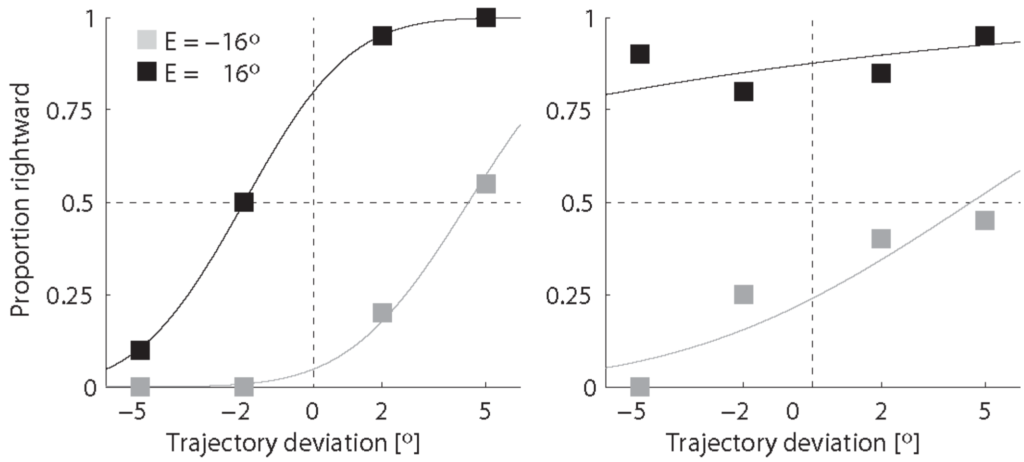

Figure 2 Illustrative performance of two participants. Data fitted with cumulative Gaussians (grey and black continuous lines). Most participants, as that represented on the left, had significant modulation of proportion of rightward responses with trajectory deviation, and the parameters of the cumulative Gaussian fits were well determined. Some psychometric functions, as that on the right panel corresponding to E = 16°, did not differ significantly from a constant and the resulting Gaussian fits were not reliable. For such psychometric curves, the nonparametric measures (bias and sensitivity) were well defined.

Although the deviation of the trajectory with respect to the trunk was independent of eye direction, we found a clear effect of eye direction on the proportion of rightward reports. Most recordings showed an effect of eye direction as measured by the difference in total count of rightward responses when fixating the right and left LEDs, 12/13 for alternating fixations (paradigm A), 6/7 for eccentric fixations in the dark, 10/11 for sustained eccentric fixations (paradigm C) and 14/15 for alternating fixations in paradigm D. From these, all but one showed a significantly higher number of rightward reports when looking right.

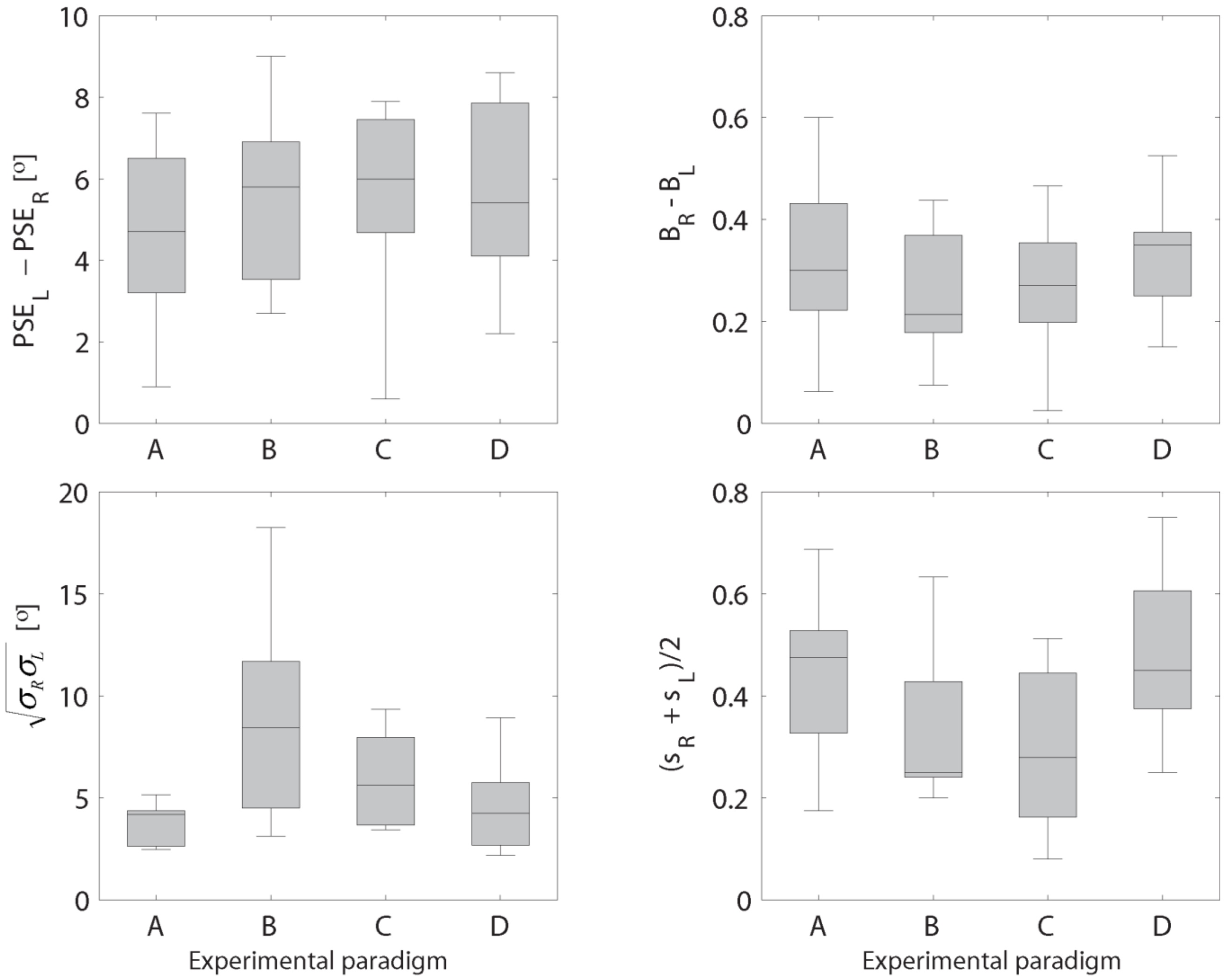

Figure 3 Changes in the psychometric curves elicited by eccentric eye positions characterized by the shift of the point of subjective equivalence (*PSE*, top left) obtained from the parametric fits, the change in average rightwards reports (non-parametric measure, top right). Overall measures of the detection thresholds (bottom left), and sensitivity (bottom right). The box plots represent median values and the first and third quartiles for each of the four experimental paradigms with centered head-on-trunk (See Methods for the description of the four paradigms: A-D).

Figure 3 summarizes the characterization of the psychometric curve pairs in paradigms A through D. It shows the shift in *PSE*: $PSE_L - PSE_R$, the change in Bias: $B_R - B_L$, as well as measures of threshold: $\sqrt{\sigma_R \sigma_L}$ and sensitivity: $(s_R + s_L)/2$. The distributions of $PSE_L - PSE_R$ and $B_R - B_L$ for different paradigms showed a big overlap, and medians had similar values (see Table 1). A Kruskal-Wallis ANOVA test did not find significant differences among paradigms for $PSE_L - PSE_R$ (χ^2_3 = 1.09, n = (10, 7, 7, 14), P = 0.78) or $B_R - B_L$ (χ^2_3 = 0.94, n = (13, 7, 11, 15), P = 0.82). Threshold and sensitivity do show some differences (figure 3 C and D, Table 1) suggesting that task difficulty was lowest for alternating fixations and highest when eye eccentricity was maintained in the dark. The Kruskal-Wallis ANOVA test found that the differences for $1\ \sqrt{\sigma_R \sigma_L}$

were not statistically significant (χ_3^2 = 7.68, n = (10, 7, 7, 14), P = 0.053), but that those for $(s_R + s_L)/2$ were (χ_3^2 = 9.61, n = (13, 7, 11, 15), P = 0.022). When data from paradigm A and the eccentric position data from paradigm D were pooled (the experimental conditions for eccentric trials in D were the same as in paradigm A), the effect of the paradigm was significant for $1/\sqrt{\sigma_R \sigma_L}$ (χ_2^2 = 7.4, n = (24, 7, 7), P = .025) and $(s_R + s_L)/2$ (χ_2^2 = 9, n = (28, 7, 11), P = 0.011). Tukey's honestly significant difference test at the 0.05 significance level found differences in the mean rank of $1/\sqrt{\sigma_R \sigma_L}$ between alternating fixations ([A,D]) and dark fixations (B), and in the mean rank of $(s_R + s_L)/2$ between alternating fixations ([A,D]) and sustained fixations (C). Taken together, the group comparisons for the four quantities of interest suggest that the difference in difficulty did not translate into a clear difference in $PSE_L - PSE_R$ or $B_R - B_L$.

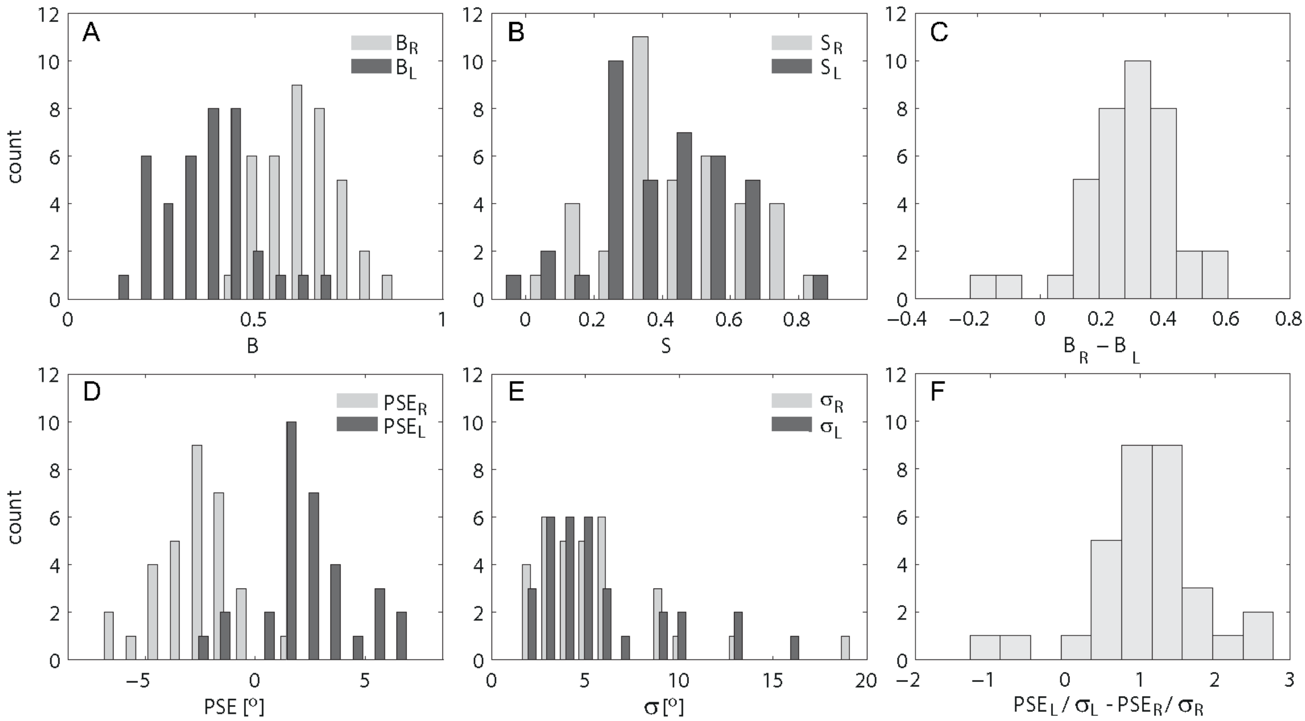

Figure 4 Histograms of data pooled across all paradigms with centered head-on-trunk. Nonparametric measures on the top row (A-C) and parametric measures on the bottom row (D-F). Panels C and F are the paired comparisons of the same data represented on panels A and D, respectively. Not only the paired differences peak away from zero (C and F), but the population distributions (A and D) have a small overlap.

Figure 4 shows the population distributions pooled across the four paradigms. As expected from symmetry considerations, there was no significant difference between looking right and left (E = 16° and E = -16°) for precision (W = 14, n = 32, P = 0.85, Wilcoxon signed-rank test) or sensitivity (W = 14, n = 38, P = 0.14, Wilcoxon signed-rank test) and there was a high degree of overlap between the right and left populations as quantified by the cosine similarity (non-centered Pearson correlation coefficient) of the two histograms (r = 0.94 and r = 0.72 respectively). The effect on *PSE* and *B* on the other hand is substantial. Not only was the distribution of paired differences significantly different from zero (W = 2, n = 32, P = 2.5e-7 and W = 2, n =38, P =5.4e-9 respectively, Wilcoxon signed-rank test) but the two distributions were well separated, with cosine similarity coefficients of r = 0.18 for both *PSE* and *B*. Across the four paradigms $PSE_L - PSE_R$ varied between -3.3° and 9° with a median of 5.3° and the 95% confidence derived from bootstrapping with 1000 iterations was between 4.3° and 6.15°. $B_R - B_L$ varied between -0.22 and 0.60 with a median of 0.3 and a 95% confidence interval between 0.23 and 0.35.

The average pooled psychometric curves are shown in Figure 5 together with the average difference between the two as a function of trajectory deviation. In principle, the observed change in the proportion of rightward responses could be due to a horizontal shift of perceived direction of motion (or direction of the subjective median plane of the trunk) or by biasing the response towards the direction of eye eccentricity in lapse trials. The first explanation leads to a horizontal shift of the psychometric curves while the second would predict a vertical shift, and the difference in the proportion of rightward responses would not depend on trajectory deviation. Since the effect of trajectory deviation was significant (χ^2_3 = 17.3, n = 32, P = 6e-4, Friedman test), we conclude that, at least at the population level, the result was not simply due to an effect on lapse trials or to a non-specific increase to report in the direction of eye deviation.

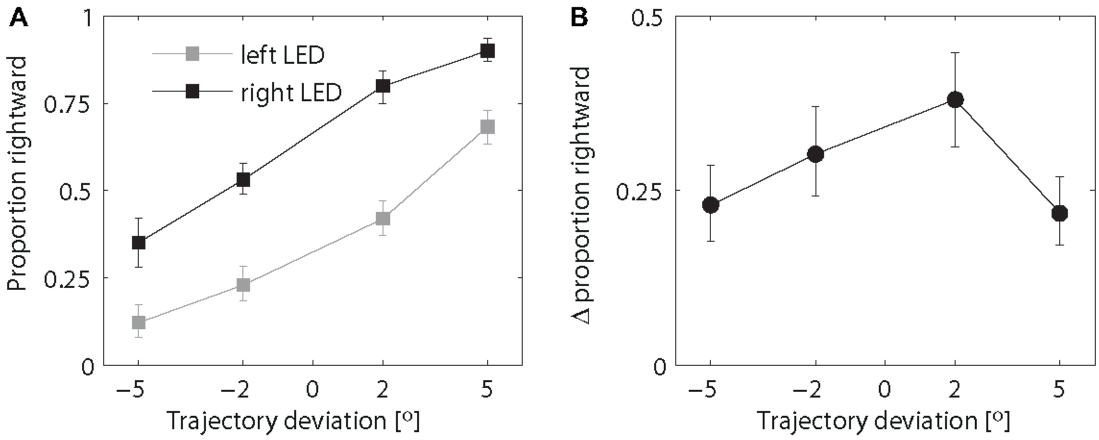

Figure 5 A: The proportion of rightward responses averaged over all 32 subjects in the head centric paradigms. When subjects participated in several paradigms, a within-subjects average was done prior to the average across subjects. B: average of intra-individual differences in rightward reports. The difference in reports when looking right and left is maximal for trajectories close to straight-ahead and decreases for larger trajectory deviations. In both panels error bars represent the 95% confidence interval as estimated from bootstrapping the data with 500 repetitions.

Centered versus deviated eye-in-head

The results from the previous paradigms suggested that eye deviation shifts either the point of subjective equivalence or the median plane of the trunk. In this paradigm we asked whether eye eccentricity also affects the uncertainty in the task. A higher uncertainty would be reflected in higher σ and lower sensitivities when compared with centric eye fixation. A group of subjects performed the task with blocks that had alternating left and right eccentric fixations and blocks in which gaze was always guided towards a center LED. Figure 6A shows the pooled psychometric functions (including the three subjects that showed the reversed eye eccentricity effect) together with the values of precision and sensitivities. We combined the two eccentric values, computed log($\sqrt{\sigma_R \sigma_L}$) and compared it to log(σ_C) obtained from the psychometric curves with a centered fixation target (Figure 6B). The difference log ($\sqrt{\sigma_R \sigma_L}$)-log σ_C ranged from -1.3 to 0.7 with a median of -0.14 and was not significantly different from zero (W = 6, P = 0.8, n = 14 , Wilcoxon sign rank test). The difference in sensitivities was not significant either (W = 7, P = 1, n = 15, Wilcoxon sign rank test); $(s_R + s_L)/2 - s_C$ varied between -0.3 and 0.3 with a median of -0.05. We therefore conclude that eye direction did not affect the sensitivity to motion direction.

Since this paradigm included both centric and eccentric eye-in-head it was possible to assess the symmetry of the effect. The difference between the effect of leftward eye deviation $PSE_L - PSE_C$ (2.6° +/- 0.7°; mean +/- SEM) and rightward eye deviation $PSE_C - PSE_R$ (1.9°+/- 0.6°) was not statistically significant (t_{13} = 0.75, P = 0.47, two tailed paired Student's t-test). The same was true for the Bias measure; the average values of $B_L - B_C$ (-0.14 +/- 0.04; mean +/- SEM) and $B_C - B_R$ (-0.12 +/- 0.03), were not significantly different (t_{14} = -0.59, P = 0.56, two-tailed paired Student's t-test).

Finally we estimated the weight of the eye contribution. We fitted the three psychometric curves for each subject using a single set of parameters and assuming that the estimated direction can be written as $\hat{\theta} = \theta + aE + b$ where b is a constant bias (the three fit parameters were a , b and σ). This is equivalent to setting $PSE = -aE - b$. We obtained a = 0.17 (0.06) (median and median absolute deviation). The correlation coefficient between $a\Delta E$ ($\Delta E = 32°$) and $PSE_L - PSE_R$ was = 0.95 and between σ and the geometric mean of σ_L , σ_C and σ_R r = 0.98.

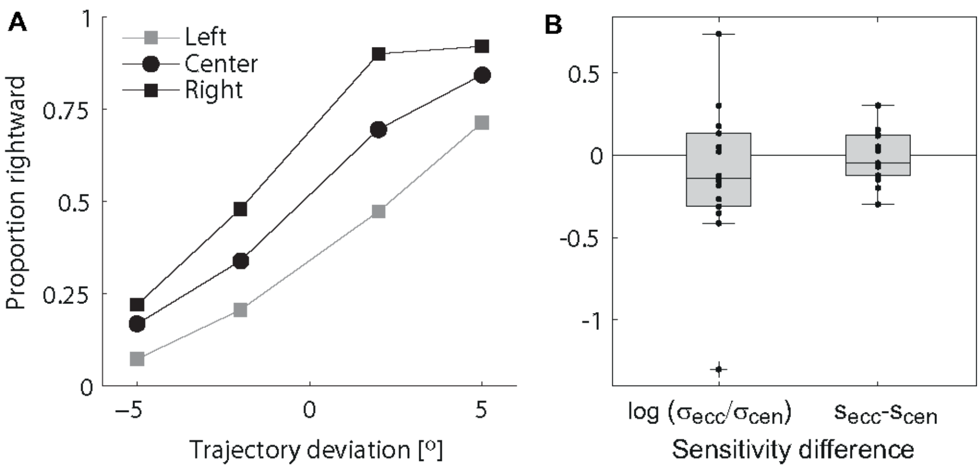

Figure 6 Paradigm with eccentric and centric eye positions. The goal was to determine whether eye eccentricity also changes sensitivity. A: average psychometric curves across all the subjects in the paradigm. B: the difference in sensitivity as quantified by log σ and the nonparametric measure *s*. Individual data is superimposed on the boxplot. The median log σ was lower for the eccentric conditions, but the difference was not statistically significant.

The effect of head-on-trunk deviation

We next asked whether head-on-trunk direction would have a similar effect on vestibular direction discrimination. To that end, another group of subjects performed the experiment with head-on-trunk displaced to the left 16° (Figure 1). Eccentric head-on-trunk (H = -16°) combined with a centric eye-in-head (E = 0°, gaze aligned with the head) when fixating the left LED, and with an eccentric eye-in-head (E = 16°, gaze aligned with the trunk) when fixating the center LED. As in paradigms A and D one of the two LEDs stayed on during motion (left or center in pseudo-random order in consecutive trials). Only one participant missed a few trials (four). All but one of the 17 subjects showed a significant effect of eye position on the total number of rightward reports. **In 13 out of the 17 datasets the proportion of rightward reports was higher for E = 16° than for E = 0°, but 3 out of 17 showed the reversed effect. Since we were interested on the effect of head eccentricity, we excluded the participants with reversed eye effect from further analysis to minimize the impact of such a confounding factor. Therefore, the following analysis excludes the three reversed datasets. This left 13 parametric and 14 non-parametric datasets.**

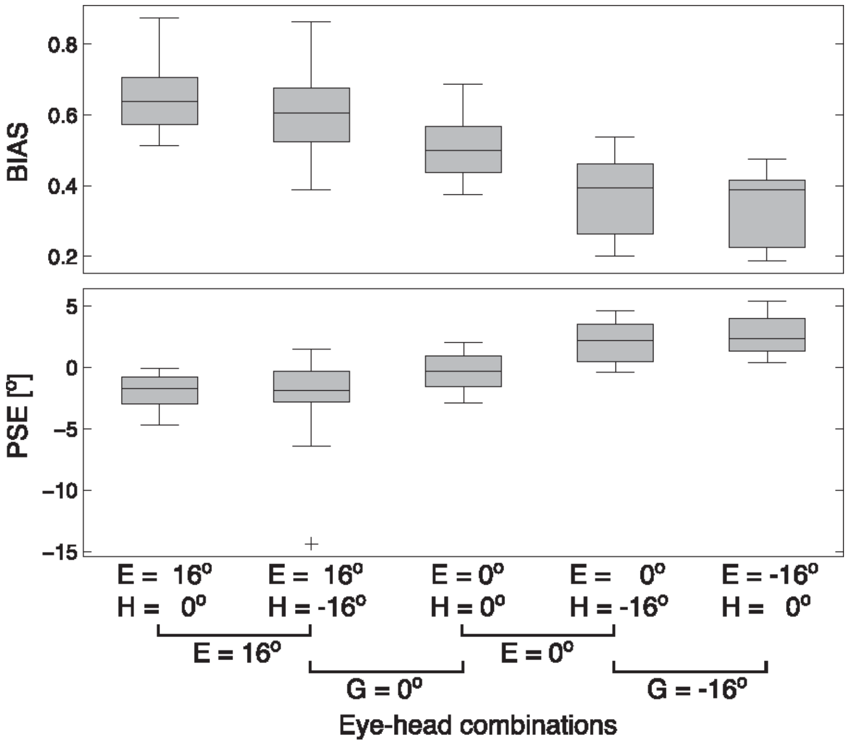

Figure 7 Bias and *PSE* with different combinations of eye and head directions. Data came from three datasets: (E=0˚,H=0˚) data from paradigm D, (E=16˚, H=0˚) and (E=-16˚, H=0˚) from paradigm A, and (E=0˚, H=-16˚) and (E=16˚, H=-16˚) from the head eccentric paradigm. With centered eye-in-head (E=0˚), there was a significant difference between the head centric and eccentric conditions. The two conditions with gaze to the left (G = -16˚) did not differ substantially providing evidence that gaze (the combination of eye-in-head and head-on-trunk) might be the determining factor. However, when looking at the condition with both eye- and head-deviations the distribution overlapped those with the same eye position (E=16˚, H=0˚) and same gaze (E=0˚, H=0˚) and the median value was not substantially different from the condition with the same eye position, indicating that the combination of eye and head eccentricity was highly variable across subjects.

To determine the effect of head eccentricity we compared the results in this paradigm with those in the two head-centered paradigms with alternating gaze directions (A and D). The datasets in paradigm A (10 parametric, 13 non-parametric) contributed the data for comparison with the H = 0°, E = +/-16° conditions, and the datasets in paradigm D (14 parametric, 15 non-parametric) the data for comparison with H = 0°, E = 0°. In the following *n* refers to the number of datasets in a given group.

First, to isolate the effect of head deviation we compared centric eye conditions (E = 0°) with and without head deviation. *PSE* (H = -16°, E = 0°) was between -0.4° and 4.6° with a median of **2.2**°. The median *PSE* with head eccentric **(n = 13)** deviated **2.5**° to the right with respect to head centric (H = 0°, E = 0°, **n = 14**) (χ_1^2 = **10**, *n* = (**13**, 14), *P* = **0.001**, Kruskal-Wallis test). Thus for E = 0°, a deviation of the head to the left shifted the psychometric curve to the right (higher proportion of leftward reports), that is, in the same direction as the shift due to eye deviations for most subjects described in the previous sections. There was a corresponding shift in the bias measure, which varied between 0.38 and 0.69 with a median of 0.5 with centered head (**n = 15**), and from 0.2 and 0.54 with a median of 0.39 with head eccentric (**n = 14**). Therefore, with head deviated to the left, the proportion of rightward responses was 20% smaller (χ_1^2 = 8.8, *P* = 0.003, *n* = (14,15), Kruskal-Wallis test). We conclude that head eccentricity affected the proportion of rightward reports in the same direction as eye eccentricity did. Indeed, the difference in *PSE* median values when comparing the same gaze conditions attained with only head deviation (E = 0°, H = -16°, **n = 13**) or only eye deviation (E = -16°, H = 0°, **n = 10**), (columns 4 and 5 in Figure 7), was only **-0.1**° (χ_1^2 = **0.5**, *n* = (**13**, 10), *P* = **0.49**, Kruskal-Wallis test).

Finally, we compared the condition with simultaneous eye and head deviations (H = -16°, E = 16°) to the head-centric results with the same eye position (H = 0°, E = 16°) or same gaze (H = 0°, E = 0°). If the effects of eye and head were of the same size and independent, we should recover the head effect mentioned above for the first comparison and should find no difference for the second comparison. For the same eye position, the difference in median *PSE* was **-0.15**° (χ_1^2 = **0.015**, *n* = (**13**, 10), *P* = **0.90**, Kruskal-Wallis test), while the difference in bias was -0.03 (χ_1^2 = 1.0, *n* = (14, 13), *P* = 0.31, Kruskal-Wallis test). For the comparisons with the same gaze the difference in median *PSE* was **-1.5**° (χ_1^2 = **3.1**, *n* = (**13**, 14), *P* = **0.081**, Kruskal-Wallis test) and the difference in bias 0.11 (χ_1^2 = 4.8, *n* = (14, 15), *P* = 0.029, Kruskal-Wallis test).

In summary, we found an effect of head direction that looked like the effect of eye direction but only when head deviation was not simultaneous with eye deviation. In the condition with both head and eye deviations, the effect of eye direction was stronger.

Discussion

Summary and relation to results in the literature

Both the direction of eye-in-head and the direction of head-on-trunk affected subjective reports about motion direction during passive translations. Although the deviation of the trajectories with respect to the trunk was the same across eye and head directions, most participants were more likely to judge a motion as 'to the right' with respect to their trunk when eyes deviated to the right, and more likely to judge motion as 'to the left' when eyes deviated to the left. Likewise, we found evidence that with leftward head-on-trunk there were more reports to the left. Only a few subjects showed a significant and opposite effect of eye/head direction. The observed changes in the proportion of rightward reports were consistent with a shift of the perceived direction of motion towards the eye/head (or a shift of the internal representation of the trunk straight ahead in the opposite direction). At the population level there was no bias when eye, head and trunk were aligned; and the shift, although in opposite directions, was of the same magnitude for right and left eye deviations (Figure 7A). Despite introducing a shift in heading perception, eye deviation had no measurable effect on the uncertainty of the task; sensitivities and thresholds were not significantly different when comparing centered and deviated eye conditions. Assuming that the point of subjective equivalence can be written as $PSE = a\mathrm{E} + b$, we were able to estimate the weight of eye deviation, $a = 0.17$ (0.06) (median and median absolute deviation).

This is the first time that shifts evoked by eye- and head- direction are reported in a task involving the perception of linear motion direction based on vestibular cues. However, the effect of eye eccentricity is well documented in auditory and visual localization and in the perception of the head straight ahead (Bohlander, 1984; Lewald, 1997; Lewald & Ehrenstein, 2000a; Razavi et al.,2007; Cui et al., 2010) and so is the effect of head eccentricity (Lewald & Ehrenstein, 1998; Lewald et al., 2000b). Moreover, the effects of eye- and head-eccentricity are equivalent in their influence on visual and auditory stimuli (Lewald et al., 2000b). When eye- or head-eccentricity is of short duration, the auditory median plane and perceived straight ahead of the head shift in the direction of eccentric gaze. This leads to a shift of free-field sound localization in the opposite direction (Lewald&Geltzmann, 2006). However, when eye position is maintained eccentrically for longer periods both perceived head straight ahead and perceived free-field sound localization shift toward eye eccentricity with a larger shift of perceived straight ahead than sound localization (Cui et al., 2010).

Our task shares some features with acoustic localization, since the acoustic signal, like the otolith signal, is head-fixed. Acoustic localization tasks are frequently assessed with respect to the head or the eye, but some use pointing tasks, which implicitly require a trunk-based reference frame and therefore can be compared with our results. Under these conditions Lewald & Geltzmann (2006) report a shift of free-field sound localization away from eye eccentricity, while Cui et al. (2010) find an effect in the opposite direction, which increases in magnitude with a time constant of ~ 1 minute and can get as large as 40% of eye eccentricity. The shift in our psychometric curves was on average in the direction of Cui et al. (2010) but more modest in magnitude: median ΔPSE approx. 5° for a change in eye position of $\Delta\mathrm{E}$ approx. 32°, even when eccentric eye position was maintained for 6 minutes (paradigm C). This suggests that the effect of eye eccentricity might be modality dependent. In agreement with Cui et al. (2010), we found that the effect was not dependent on the presence of a visual stimulus, eye deviation alone was sufficient to evoke it.

The one-interval forced choice task used in our experiments involves the comparison of the representation of motion direction and the representation of the trunk perceived straight ahead. In addition, reference frame transformations are needed to integrate sensory information originating in different reference frames: for example, the trunk for most somatosensory information and the head for otolith information. Therefore, the observed shift could come from errors in any of these three components: direction of motion, straight ahead representation, and/or reference frame alignment. Head and trunk reference frame misalignment might make a contribution since perceived head straight ahead deviates towards eccentric eye position, suggesting an illusory head-on-trunk deviation (Lewald&Ehrenstein, 2000a, Cui et al., 2010).

Although we describe eye direction and head direction effects, we cannot determine direct causation. For example, there's evidence that the locus of attention is one of the factors that shifts the auditory median plane (Bohlander, 1984) and might also contribute to the shifts observed here. Attention was likely focused in the direction of gaze prior to movement onset. However, during the translation the participants concentrate on their feeling of motion with respect to the trunk which might shift the locus of attention toward the trunk.

In the following sections we discuss several ways in which eye direction could affect inertial heading discrimination.

Effect of eye movements and visual input

Since eye deviation influenced direction discrimination, an influence of eye movements cannot be excluded a priori. The possibility needs to be considered because eye movements could be elicited during motion by the linear vestibulo-ocular reflex (LVOR) (Raphan & Cohen, 2002). Since the deviation of eye-in-trunk is larger than the deviation of the path, the LVOR would move the eyes leftward when looking left and rightward when looking right. However, eye movements were too small to account for the effect. In all but one of the experimental paradigms the LED was on during motion, which leads to visual cancellation of the LVOR. Although we did not record eye movements in the paradigms with LED on during motion, we expect participants to maintain fixation successfully (nobody reported any difficulty in looking at the LED) and have only minimal eye movements, smaller than those in the LED off paradigm, which were recorded for three of the participants and were substantially less than 1 degree in amplitude and were not correlated with the *PSE* shift. This suggests that the largest effect is related to eye position and not to eye movements. Van Barneveld and Van Opstal (2010) also found a primary effect related to eye position rather than eye velocity on the perceived auditory median plane.

It could also be argued that the presence of the LED makes a contribution. Since the LED was mounted on the motion platform, it gave no information about motion. However, it the brain would assume that the LED is space-fixed, the fact that its retinal image remains stationary would only be consistent with a trajectory in the direction of the LED. Multisensory integration of the gaze dependent signal with more veridical somatosensory and vestibular signals would result in a shift of the estimates towards gaze. Monkeys and humans combine directions approximately in inverse proportion to their uncertainty (vestibular signals are overweighted) when the estimates from the visual system (based on expanding optokinetic patterns) and the vestibular system differ (Fetsch el al., 2009; Butler et al., 2010). Although this seems plausible, the paradigm in which the LED was turned off during motion shows that it cannot be the main contribution, since the effect in both *PSE* and *B* was similar to the paradigm with LED ON during motion (compare paradigms A and B in Figure 3).

Efferent copies of motor commands could also constitute a confounding factor. In most paradigms there was a gaze shift from the center LED to the peripheral LED before movement onset. In free gaze shifts eye and head components are inextricable. Although the head of the participants is fixed with a mask and cannot move, the eye movement might be accompanied by a head motion command and an efference copy that could be used by the brain to update the estimate of head-on-trunk, which would transiently deviate in the direction of the eye position change. In this case, the effect would come from a change in eye position and not from eye position itself. Although such a transient effect might exist, one of our paradigms had subjects looking eccentrically without breaking fixation. Even without eye movements we observed eye direction related shifts in the psychometric curves.

Altogether, our results suggest that the largest effect was related to eye position and not to eye movements or the presence of a visual target.

Reference frame transformation

To perform the one-interval forced choice task, participants had to compare the perceived direction of motion with the perceived trunk straight ahead. Information about direction of motion can be extracted from a number of sensory systems but we expect the vestibular system of the inner ear to play a major role since the otoliths are dedicated linear accelerometers. Monkeys and humans do show a decreased performance level when the vestibular system is compromised (Gu et al., 2007; Valko et al., 2012). Somatosensory information is immediately available in trunk-referenced coordinates but vestibular signals are encoded in a head-fixed frame and a reference frame transformation (implicit or explicit) is needed: $d_T = d_H + \hat{H}$. $\hat{H}$, the estimate of head in trunk deviation, is the signal needed for this transformation and it deviates in the direction of eccentric eye position when the head is centered on the trunk (Lewald et al., 2000a; Cui et al., 2010), which can be represented as $\hat{H} = aE$. Therefore d_T would also deviate toward eye position. This could explain the effect of eye eccentricity. Errors in head-to-body transformations have also been proposed to explain gaze dependent deviations in reaching (McGuire and Sabes, 2009).

The effect of head-on-trunk direction would also be explained by errors in the reference frame transformation if head eccentricity is overestimated, as is the case in auditory localization. In that case, the subjective median plane of the head shifted in the direction of eccentric head (Lewald et al., 2000b). Consequently, a leftward head eccentricity would lead to an increase in leftward reports, as observed for most participants.

The physical quantities of interest can be simultaneously represented in several reference frames (McGuire &Sabes, 2009). Since translations change the position of the participant in space, the use of allocentric representations might be advantageous. Direction discrimination would then involve the comparison of the orientation of the trunk in space and the estimated direction of translation in space. Although in the dark there is no sensory signal providing the orientation of the body in space, which is needed to bridge the gap between the egocentric sensory signals and an allocentric representation, cognitive knowledge about the setup and estimates from the head direction system, which represents the head orientation in space (Taube et al., 1990) could provide this information. We expect a contribution to the observed errors from an allocentric representation of the task primarily in the head-eccentric experiments, in which the neck proprioceptive signals decay with time, making cognitive factors about the spatial experimental setup more relevant.

Effect of biases

Our brains are tuned to perform in our natural environments, which include a rich sensory content and statistical regularities. Regularities are also present in our behaviors; despite the many degrees of freedom available in principle, behaviors tend to be stereotyped in practice. For example, a gaze shift ΔG can be achieved by an infinite number of combinations of eye and head shifts as long as $\Delta E + \Delta H = \Delta G$. However, free gaze shifts display a relatively tight relation between ΔE and ΔH (for a review see Freedman, 2008) and the final gaze deviation is mostly contributed by head-on-trunk. Likewise, there are many feasible ways to move between two points; walking forward, sideways, with gaze up, down, to the sides, etc. However, humans tend to align body, head and eye in the direction of motion when walking straight and gaze anticipates the future direction of locomotion just before a change in direction (Hollands et al., 2002). The brain can use such regularities to supplement incoming sensory information.The Bayesian framework provides a principled way to implement prior information (Kording and Wolpert, 2004) and has been applied to explain several aspects of perception (Ernst & Banks, 2002; Weiss et al., 2002; Laurens et al., 2011). In this framework priors reflect statistical regularities and correlations occurring during natural behavior. The use of prior information or biases probably plays a bigger role in situations in which the sensory input is poor, as is the case in many experiments explicitly designed to isolate contributions of individual sensory systems. Relying on priors leads to errors in situations that depart considerably from physiological conditions, but it leads to smaller mean squared errors on the whole, since it weighs physical situations according to their 'a priori' frequency.

Bayesian inference has already been applied to vestibular and visuo-vestibular processing (Fetsch et al., 2009; Butler et al., 2010; Laurens et al., 2011), and priors, in particular, have been used to explain several perceptual phenomena and illusions taking into account the full dynamics and the kinematic laws of motion in a gravitational field (Laurens & Droulez, 2007).

Here we present a simple static Bayesian inference process to illustrate how priors representing statistical regularities in natural behaviors, can introduce a spurious dependence of the estimated trajectory-in-trunk deviation on eye and/or head deviation even when the physical stimulus does not contain such dependencies.

The estimates are based on sensory evidence supplemented by prior information. Mathematically they are based on the log of the a posteriori distribution (assuming Gaussian distributions it is possible to calculate the Bayesian estimates analytically):

$$I = -\frac{(s_v - d_T + H)^2}{2\sigma_v^2} - \frac{(s_n - H)^2}{2\sigma_n^2} - \frac{(s_e - E)^2}{2\sigma_e^2} + I_{priors} \qquad \textbf{(7)}$$

The first three terms represent accurate sensory information. This expression includes the three physical variables: E (eye-in-head), H (head-on-trunk) and d_T (direction of translation with respect to the trunk). Sensory information includes: s_e (eye-in-head, from efference copies of motor commands and proprioception), s_n(head-on-trunk, only available from neck proprioceptors in our experiments) and s_v, a vestibular signal with information about the direction of translation with respect to the head, which can be related to d_T by the head-on-trunk: $d_H = d_T - H$. Assuming that sensory information is accurate on average, we obtain: $\langle s_v \rangle = d_T - H$, $\langle s_n \rangle = H$, $\langle s_e \rangle = E$, where brackets denote the mean over repeated presentations of the same stimulus.

We consider two behavioral regularities that could in principle introduce correlations between direction of motion and eye/head deviation. We derive the Bayesian estimate and then report its average over trials,$\langle \tilde{d}_T \rangle$, which is a function of the physical variables (d_T , E and H).

The first prior term we consider reflects the fact that free gaze shifts have both an eye-in-head and a head-on-trunk component. The form of the prior and the resulting average estimate $\langle \tilde{d}_T \rangle$ are:

$$I_{prior,1} = -\frac{(H-E)^2}{2\sigma_{p,1}^2}, \quad \langle \tilde{d}_T \rangle = d_T + (a-1)H + bE, \quad 0 < a, b < 1, \qquad \textbf{(8)}$$

In this Equation and in Equations 9 and 10, a and b are functions of the distribution variances $\sigma_e^2, \sigma_n^2, \sigma_v^2, \sigma_p^2$. Since $(a-1) < 0$, the average $\langle \tilde{d}_T \rangle$ shifts away from head eccentricity but toward eye eccentricity ($b > 0$). That is, under this prior, eye and head eccentricities would lead to oppositely directed biases, contrary to our results.

The second bias reflects the physiological behavior of looking where you're going (Hollands et al., 2002; Hicheur et al., 2005), which we implemented by adding a prior term that tends to align gaze with the direction of motion d_T : $\boldsymbol{G \equiv H + E = d_T}$. The prior and the average estimates in this case are:

$$I_{prior,2} = -\frac{(H + E - d_T)^2}{2\sigma_{p,2}^2}, \qquad \langle \tilde{d}_T \rangle_2 = a d_T + b(H + E), \;\; 0 < a, b < 1, \tag{9}$$

Under this prior, the effects of head and eye eccentricity on $\langle \tilde{d}_T \rangle$ are indistinguishable; $\langle \tilde{d}_T \rangle$ shifts toward both eye and head eccentricity by the same amount. This predicts that when H = -16° and E = 16° (one of the two conditions in the head eccentric paradigm), *PSE*s should be around 0°, which does not correspond exactly with our results (see 2nd column in Figure 7). Although failing in this point, it is in qualitative agreement with the other four conditions.

The $\langle \tilde{d}_T \rangle$ estimates derived from the above two priors shift in the direction of eye deviation, as observed for most participants. For a few subjects, however, $\langle \tilde{d}_T \rangle$ shifted away from eye deviation and this would arise, for example, from a prior for zero gaze: $\boldsymbol{G \equiv H + E = 0}$.

$$I_{prior,3} = -\frac{(H+E)^2}{2\sigma_{p,3}^2}, \quad \langle \tilde{d}_T \rangle_3 = d_T + (a-1)H - bE, \;\; 0 < a, b < 1 \tag{10}$$

Now the estimate $\langle \tilde{d}_T \rangle$ shifts away from both eye and head eccentricity, as was the case for the three subjects who showed the reversed effect in the experiments with head eccentric.

The above examples illustrate that behavioral regularities, possibly other than the ones suggested here, could be behind the spurious dependencies found our results. Further experiments should investigate whether the shifts are consistent with an optimal implementation of prior information and are not simply the result of inaccuracies in the estimation process. This could be done, for example, by assessing whether the magnitude of the shifts changes when the reliability of the inertial signals is manipulated. That is, one should observe a reweighting of prior and sensory information such as has been described on a trial-by-trial basis in visuo-vestibular integration (Fetsch et al., 2009).

Head eccentricity

We also found evidence of an effect of head-eccentricity on performance. In all paradigms we used the same trajectories, which were defined relative to the trunk's straight ahead. While varying gaze does not change the sensory stimulus to the otoliths, changing head-on-trunk does. With eccentric head-on-trunk the otoliths are no longer activated along the median plane but along a deviated direction leading to a non-symmetric pattern of activation.

Systematic errors in heading direction estimation related to the deviation of the path with respect to the median plane of the head have recently been reported and reported a bias toward lateral directions (Cuturi & MacNeilage, 2013), which would predict a preponderance of rightward reports when the head is deviated to the left. In a study by Ivanenko et al. (1997) subjects with head-on-trunk deviated 45° and motion along the trunk, blind pointing at the estimated direction of motion deviated from true direction by approximately 3° in the direction of the head. Estimated trunk orientation deviated even more, about 6°, also in the direction of the head. Therefore the estimate of heading relative to the estimate of the trunk straight-ahead deviated in the direction opposite of head-on-trunk position. When extrapolated to our study, both studies would predict a preponderance of rightward reports when the head is deviated to the left, opposite to our findings. However, none of these studies monitored eye position, which is known to have a strong effect in localization. Moreover, one should be cautious since estimates for a given quantity will depend on the specific task.

Another difference in our experiments between eye and head eccentric conditions is that, unlike eye eccentricity, head eccentricity was not actively maintained by the participants; therefore the only available information about head-on-trunk position was that from neck proprioceptors and the knowledge of the subjects about the experimental setup. A few subjects mentioned that, when looking at the left LED, they felt that both head and trunk were facing the LED. This suggests that at least some subjects had internalized the relative positions of the objects in the platform (Figure 1) and that the known orientation of the LED in space was used as an 'anchor'. Looking at the left LED, eye-in-head was centered, once the head-in-trunk signal has decayed the brain could interpret this situation in two ways (i) "I am looking along the trunk, therefore along the axis of the motion platform" since they know that their trunk faces the LED located straight ahead or (ii) "I am looking to an LED which I know is positioned to the left of the motion platform axis and my head feels centered on the trunk, therefore my body must be turned in the direction of the LED". If option (ii) is favored, and this same signal is used as reference for the task, there should be an increase in rightward reports (since the reference has shifted to the left). This cannot be the main contribution in the shift of the psychometric functions since the subjects that mentioned this perception still showed a preponderance of leftward judgments. Nobody reported misperception of trunk orientation when looking at the LED located straight ahead from the trunk. In this configuration the context knowledge about LED positioning, the true trunk orientation and a decayed head signal could lead, in principle, to a perception of gaze as to the right (due to the eccentric eye position signal to the right). These cognitive effects might explain why results about the effect of head direction were more variable across subjects than those of eye direction.

Across subjects, the shifts observed in the two head-eccentric conditions were almost symmetric about zero, while one would have expected an overall leftward pattern if gaze (eye-in-trunk) was the determinant factor. Here the non-balanced design of the head-eccentric paradigm, with only leftward and straight-ahead gaze, might have played a role. An initial preponderance of leftward reports might have been cancelled by an expectation of an equal number of rightward and leftward deviations that would tend to balance the total number of rightwards and leftwards reports. These differences preclude a direct comparison of the magnitude of the head and eye eccentricity effects on the heading discrimination task.

Origin of relevant eye and head position signals

Theoretically, the signals of eye position stem from two different sources: efference copies of motor commands ("outflow" or corollary discharge) and extra-ocular muscle (EOM) proprioception ("inflow") (Donaldson, 2000; Ruskell, 1999). The outflow signal is comprised of copies of motor commands sent to the EOM, and should project to sensory pathways simultaneously (Crapse and Sommer, 2008a; 2008b). Previous research indicated that the efference copy provides a majority of the eye position information by on-line feedback (Guthrie et al., 1983; Lewis et al., 2001); while the afferent signals from the EOM may also provide complementary eye position information (Weir et al., 2000).

In the case of head-on-trunk, both neck proprioception and efferent copies from motor commands to move the head can provide the necessary information. In our experiments the head was not free to move, therefore neck proprioception was the only direct sensory input available. Eccentric head-on-trunk was kept continuously for at least 12 minutes, which leads to adaptation and a decreased perception of head deviation.

Conclusion

We have reported for the first time an effect of eye and head direction on inertial motion direction discrimination. So far, effects of eye and head eccentricity were reported in localization tasks involving visual and/or auditory stimuli. Both source localization and heading direction estimation rely on cues from different sensory systems in different reference frames. We hypothesize that the systematic errors observed in both kinds of tasks occur because the underlying reference frames, which are referenced to eye, head or trunk, deviate from their configurations during natural behaviors. This is consistent with ideas about predictive coding and Bayesian inference in general, which propose that perception is not a pure bottom-up process, but a process incorporating contextual information and expectations (Friston, 2005). If this is the case, systematic errors with eccentric eye and/or head might be universal, while their instantiation could differ because their expected configurations might differ depending on the nature of the task.

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Abreviations

EOM: extra-ocular muscle. LED: light emitting diode. MAD: median absolute deviation. MLE: maximum likelihood estimate. LVOR: linear vestibulo-ocular reflex. PSE: point of subjective equivalence. SEM: standard error of the mean.

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Tables

Table 1 Effect of gaze direction on the psychometric functions

Characterization of the effect of eye deviation on the location parameters of the psychometric curves $PSE_L - PSE_R$ and $B_R - B_L$, as well as characterization of the overall sensitivity $\log\sqrt{\sigma_R\sigma_L}$ and $(s_R + s_L)/2$. A, B, C, D refer to the four paradigms with centered head-on-trunk. **A: randomly alternating right and left eye deviations, LED ON during motion. B: randomly alternating right and left eye deviations, LED OFF during motion. C: long duration right and left eye deviations, LED ON during motion. D: paradigm including E = 0°, LED ON during motion. (Full description in the Methods section.)**

			A	**B**	**C**	**D**
Parametric measures	$PSE_L - PSE_R$ (deg)	median	4.7	5.8	6.0	4.8
		average	4.7	5.6	5.5	4.6
	$\log\sqrt{\sigma_R\sigma_L}$ σ in deg	median	2.9	4.3	3.5	2.9
		average	2.6	4.1	3.4	2.8
	n		10	7	7	14
Nonparam. measures	$B_R - B_L$	median	0.30	0.21	0.27	0.32
		average	0.32	0.26	0.27	0.26
	$(s_R + s_L)/2$	median	0.47	0.25	0.28	0.45
		average	0.43	0.34	0.29	0.51
	n		13	7	11	15