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Vestibular cognition: the effect of prior belief on vestibular perceptual decision making

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Abstract Vestibular cognition is a growing field of interest and relatively little is known about the underlying mechanisms. We tested the effect of prior beliefs about the relative probability (50:50 vs. 80:20) of motion direction (yaw rotation) using a direction discrimination task. We analyzed choices individually with a *logistic regression model* and together with response times using a *cognitive process model*. The results show that self-motion perception is altered by prior belief, leading to a shift of the psychometric function, without a loss of sensitivity. *Hierarchical drift diffusion analysis* showed that at the group level, prior belief manifests itself as an offset to the drift criterion. However, individual model fits revealed that participants vary in how they use cognitive information in perceptual decision making. At the individual level, the response bias induced by a prior belief resulted either in a change in starting point (prior to evidence accumulation) or drift rate (during evidence accumulation). Participants incorporate prior belief in a self-motion discrimination task, albeit in different ways.

Keywords Vestibular cognition · Anticipation · Bias · Direction recognition · Drift diffusion model · Expectation · Perceptual decision making

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Introduction

Whole body motion perception involves vestibular sensory information. While earlier studies on motion thresholds focused on sensory transduction processes [1], it became clear that perceptual thresholds do not reflect low-level sensory processes alone. Perception involves non-sensory components, and recently, Merfeld and colleagues [2] introduced a high-pass filtering mechanism as an important feature of decision making. Based on computational modeling studies, it has become clear that the vestibular system performs sophisticated processing based on internal models [3]. A major component of such internal models is prior beliefs. To investigate the effect of prior beliefs on vestibular perception, we focused on biased perceptual decision making. A bias can be introduced by the ability to anticipate upcoming stimuli and can be based on prior beliefs and knowledge about stimulus frequency [4]. To date, there is still relatively scarce evidence of biased perceptual decision making in the vestibular modality. A notable exception is the study by Wertheim and colleagues [5], showing that passive self-motion perception reported by participants depends on their prior knowledge about possible motion trajectories. Participants usually see the device before they take part in the experiment, and this knowledge alters the perceptual experience they report when exposed to vestibular stimuli. While those authors [5] collected verbal reports after linear passive self-motion, we measured binary choices and response times (RTs) to tap into underlying mechanisms involving prior belief.

Participants performed a yaw rotation discrimination task in two conditions. In the unbiased condition, participants were told that each motion direction was equally likely to occur; in the biased condition, participants were instructed that rightward rotations were more likely. This

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manipulation was intended to introduce a response bias. This bias manifests itself as a shift of the psychometric function, without a substantial loss of sensitivity [6]. Previous research in the visual domain has also yielded faster RTs to more frequently occurring stimuli when compared to RTs to stimuli that are shown less frequently [4]. Accuracy is also increased for more frequent stimuli. In psychophysics, it is still common to analyze choices exclusively. If RTs are collected, they are considered independently of choices; however, this approach is inadequate, since it is difficult to detect potential trade-offs. For instance, a participant may increase his probability of giving a correct answer by taking more time. Therefore, data analysis in perceptual decision making requires a joint consideration of choices and RTs.

A common model used for joint analysis of choices and RTs is the drift diffusion model (DDM) [7]. In this model, the decision-making process is based on the accumulation of noisy sensory evidence. A decision for either of the two choice alternatives is made when a lower or upper bound is reached. The rate of evidence accumulation is known as the drift rate, and the distance between the two choice alternatives is known as the boundary separation. Sensory and motor processing not directly related to the decision-making process is taken into account by the inclusion of a non-decision time. The final parameter is the starting point of the evidence accumulation process. For unbiased decision making, this lies halfway between the two alternatives; in the case of biased decision making, the starting point may be shifted toward either boundary.

In essence, the DDM offers two possibilities for introducing a bias [7]: (1) by adjusting the starting point toward the decision boundary of the more likely option or (2) by increasing the drift rate for the more likely option. Both mechanisms can account for potential influences of prior belief. A change in starting point can be interpreted as a bias prior to the accumulation of sensory evidence, which may reflect a strategic response bias, while the altered drift rate exerts its effect during the process of evidence accumulation [8].

The goal of this study is to investigate whether and how prior belief exerts an effect on passive whole body motion discrimination, similar to that found in other sensory modalities. Specifically, the question is whether participants can introduce a bias by changing their response criterion, and if so, which cognitive processes are involved. To achieve this goal, we analyzed choices using a multilevel logistic regression model, and jointly analyzed choices and RTs using a hierarchical drift diffusion model, in a simple direction discrimination task.

Methods

Subjects

Six healthy volunteers (three female/three male, aged between 22 and 29) took part in this study. Informed consent was obtained from all participants. Ethical approval was obtained from the Ethics Committee of the University of Bern.

Motion stimuli

Motion stimuli were generated using a six degree of freedom motion platform (6DOF2000E, MOOG Inc., East Aurora, NY). We used single cycle sinusoidal acceleration motion profiles with a frequency of 1 Hz. This type of yaw rotation is similar to active head movements and has been used to study passive self-motion perception [9]. Participants wore a blindfold and they were seated on a chair mounted on the motion platform. Peak velocity was individually adjusted to each participant.

Experimental procedure

The study consisted of a direction discrimination task using passive whole body yaw rotation. A high-pitched tone indicated the onset of motion. Participants were instructed to push one of two buttons to indicate their perceived motion direction as quickly as possible. In case of uncertainty, participants were instructed to guess.

Before starting the experiment, 24 practice trials with supra-threshold peak velocity were administered to allow familiarization with the task. To ensure that performance was comparable between participants, each participant's threshold [10] was determined. The main experiment consisted of 4 blocks of the same direction discrimination task, with 5 intensity levels for leftward and rightward motion, administered 12 times, resulting in 120 trials per block.

Manipulation of response bias

In the unbiased condition, participants were instructed that leftward and rightward rotations were equally likely. In the biased condition, participants were told that 80% of motion stimuli would be to the right and 20% of stimuli to the left. The conditions differed only in the instructions received; in both conditions, leftward and rightward rotations were equally likely to occur. The order of the two conditions was counterbalanced across participants.

Data analysis

Participants' choices were analyzed using a Bayesian hierarchical logistic regression model incorporating two additional parameters to account for attentional lapses and guesses [11]. We quantified a response bias as an additive effect of the biased condition on the parameter of the linear predictor. Choices and RTs were then jointly analyzed using a Bayesian hierarchical drift diffusion model [12]. All models were estimated using the brms [13] and rstan [14] R packages. We estimated several models allowing for an effect of response bias on the DDM parameters, and selected the best model based on the leave-one-out cross-validation (LOO) method [15].

Results

Probability of rightward responses

Figure 1a shows participants' proportion of rightward responses as a function of motion intensity, separately for the two instruction conditions. Motion intensity is shown as positive for rightward motion and negative for leftward motion. The scale represents the standardized peak velocity. Verbal instructions led to an overall increase in the proportion of rightward responses. This increase in rightward response probability represents a bias in perceptual decision making. Only participant 1 seems to have introduced a bias toward rightward responses at the expense of the ability to successfully discriminate between left and right; the probability of giving a rightward response is high even for trials with high leftward velocity. It is noteworthy that performance of this participant in the unbiased condition is absolutely comparable to the other participants.

Figure 1b shows the group-level parameter estimates of the logistic fit. The fixed effect for the intercept in the unbiased condition (unbiased crit) reveals that participants did not favor either of the directions, and the fixed effect of motion intensity (sensitivity) shows that stronger motion intensity increased the probability of giving a rightward response. The third and fourth parameters represent additive effects for the intercept (Δ biased crit) and slope of motion intensity (Δ biased sensitivity) in the biased condition. The additive effect on the intercept represents a shift of the psychometric curve along the x-axis, as shown in Fig. 1c. The fact that the 95% credible region lies to the right of zero means that in the biased condition, the probability of giving a rightward response was greatly increased, independently of the motion intensity. The fact that the additive effect on the slope is centered at zero means that on average, participants' altered decision criterion was not accompanied by a loss of sensitivity, resulting in similarly shaped curves in Fig. 1c. Therefore, we conclude that participants were able to incorporate the information given in the instructions into their decision-making process by shifting their decision criterion, without losing the ability to discriminate between motion directions.

Drift diffusion analysis

We next assessed whether the criterion shift shown in Fig. 1 was due to a shifted starting point or a shifted drift criterion. We estimated several DDM models, including models that allowed for an effect of the instruction condition on the boundary separation and non-decision time. Based on the LOO information criterion, we selected a model that allowed for a change in both starting point and drift rate as a function of instruction conditions. In addition, the drift rate could vary as a function of motion intensity. These were estimated as fixed effects, with random participant effects. We then compared this model, which alleviates the problem of over-fitting individual parameter estimates (partial pooling model) [12] to a non-pooling model, which estimates all parameters for each participant separately. These models were not distinguishable based on LOO. We, therefore, report parameter estimates from both models; the group-level estimates (fixed effects) are from the partial pooling model, and the individual estimates are from the no-pooling model. Figure 2a shows the estimated fixed effects for the drift rate and the starting point. The parameters are described in Table 1.

The intercept for the drift rate in the unbiased condition in Fig. 2a is slightly above zero, indicating a slightly increased probability of reaching the upper boundary. This parameter represents the amount of evidence that is accumulated independently of the motion intensity; the effect of this becomes important at low motion intensities. The additive effect on this intercept in the biased condition is greater than zero, with the 95% credible region excluding 0; this means that, at the group level, participants' drift rates for rightward motion were increased due to the instruction favoring one direction of motion. The effect of motion intensity is positive, indicating that participants incorporated information about the stimulus into their drift rates. Notably, the fixed additive effect of the biased condition on the motion intensity parameter is effectively zero. Therefore, at the group level, the biased condition does not result in altered processing of motion intensity. The starting point in the unbiased condition is zero; participants did not favor either motion direction prior to evidence accumulation. The additive effect in the biased condition is also zero, meaning that, on average, the biased condition did not result in an altered starting point.

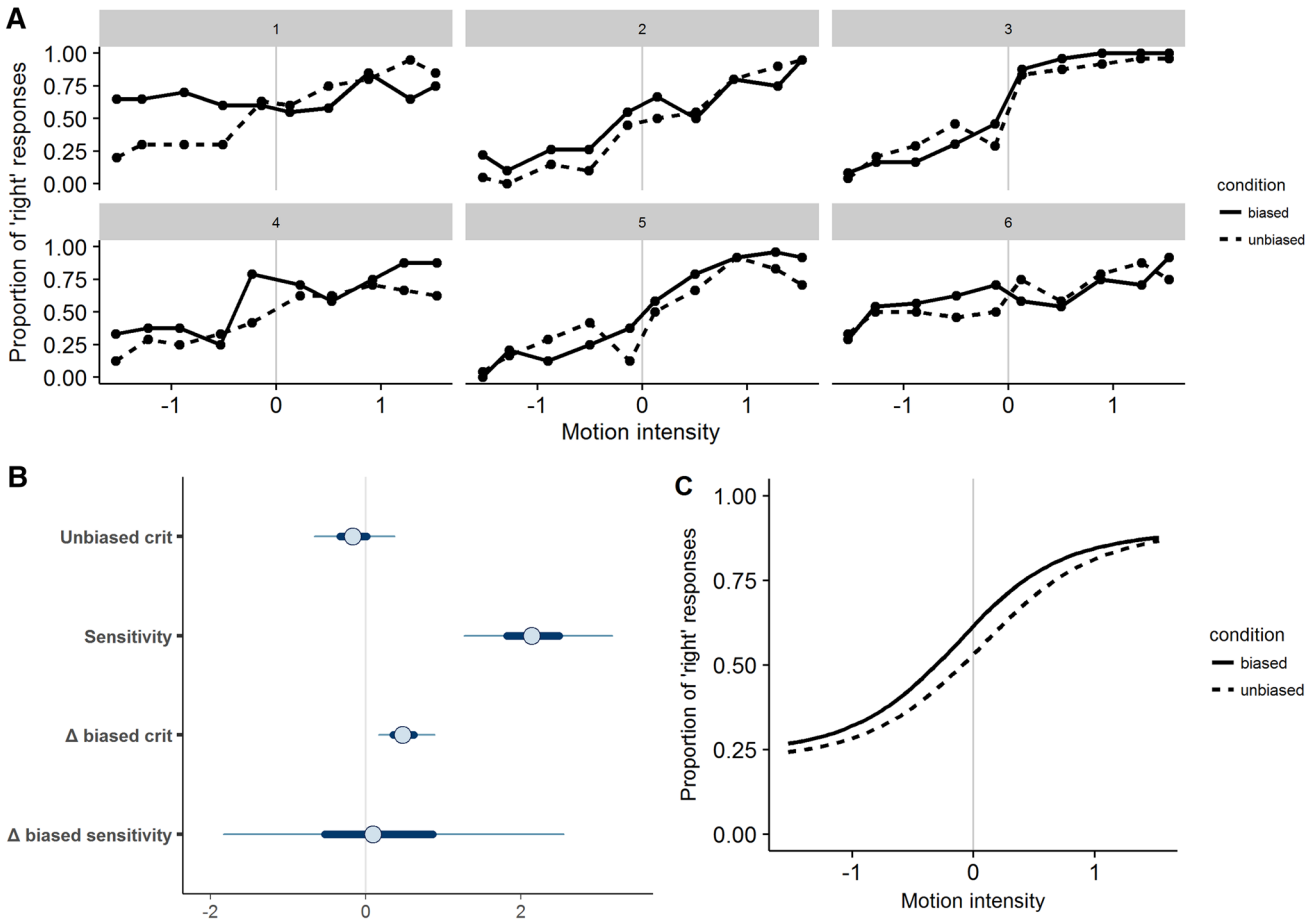

Fig. 1 Response data and hierarchical logistic regression model. **a** Proportion of rightward responses as a function of standardized motion intensity in biased and unbiased condition for all participants. **b** Median, 50 and 95% credible regions of group-level parameter estimates for the logistic fit. **c** Estimated psychometric curves for biased and unbiased condition at group level. Parameters: Unbiased crit = intercept for the unbiased condition. Sensitivity = slope parameter for the unbiased condition. Δ biased crit = additive effect on intercept for biased condition. Δ biased sensitivity = Additive effect on sensitivity for biased condition

Figure 2b shows the standard deviations of the random participant effects. Large standard deviation means that there were large inter-individual differences between participants. While the standard deviation of the additive effect on the intercept in the biased condition is relatively small, indicating that this effect is consistently found across all participants, Fig. 2b reveals that there is considerable variability between participants for both the slope of motion intensity in the unbiased condition and the additive effect on the slope in the biased condition. Since the additive effect on the slope is centered at zero, a large standard deviation indicates that there are positive and negative effects at the individual level. Any effects at the individual level may cancel out. Therefore, we report parameter estimates for each participant individually. The results are shown in Fig. 3.

The individual estimates reveal the source of variability of the effect of condition on the slope of motion intensity. Participant 1 shows a noticeable negative effect on the slope in the biased condition, resulting in a small cumulative effect of motion intensity in the biased condition; this participant does not seem to incorporate information about motion direction into the decision-making process; and this is particularly evident for leftward motion. Rather, the slight bias toward rightward responses is explained by the model as an offset to the drift rate. This offset is not visible in the unbiased condition, as the participant takes the motion intensity into account. A similar decrease in stimulus processing is visible in participant 2. The response bias in this participant is explained by an altered starting point in the biased condition. In contrast, participants 3, 5, and to a lesser extent 4 show an increased slope of motion intensity in the biased condition, coupled with an increased drift rate independent of the motion intensity. This results in both more efficient evidence accumulation for large motion intensities and a biased drift criterion toward rightward responses. Finally, participant 6 shows no effect on stimulus processing and a decreased offset in the drift rate in the biased condition. Similar to

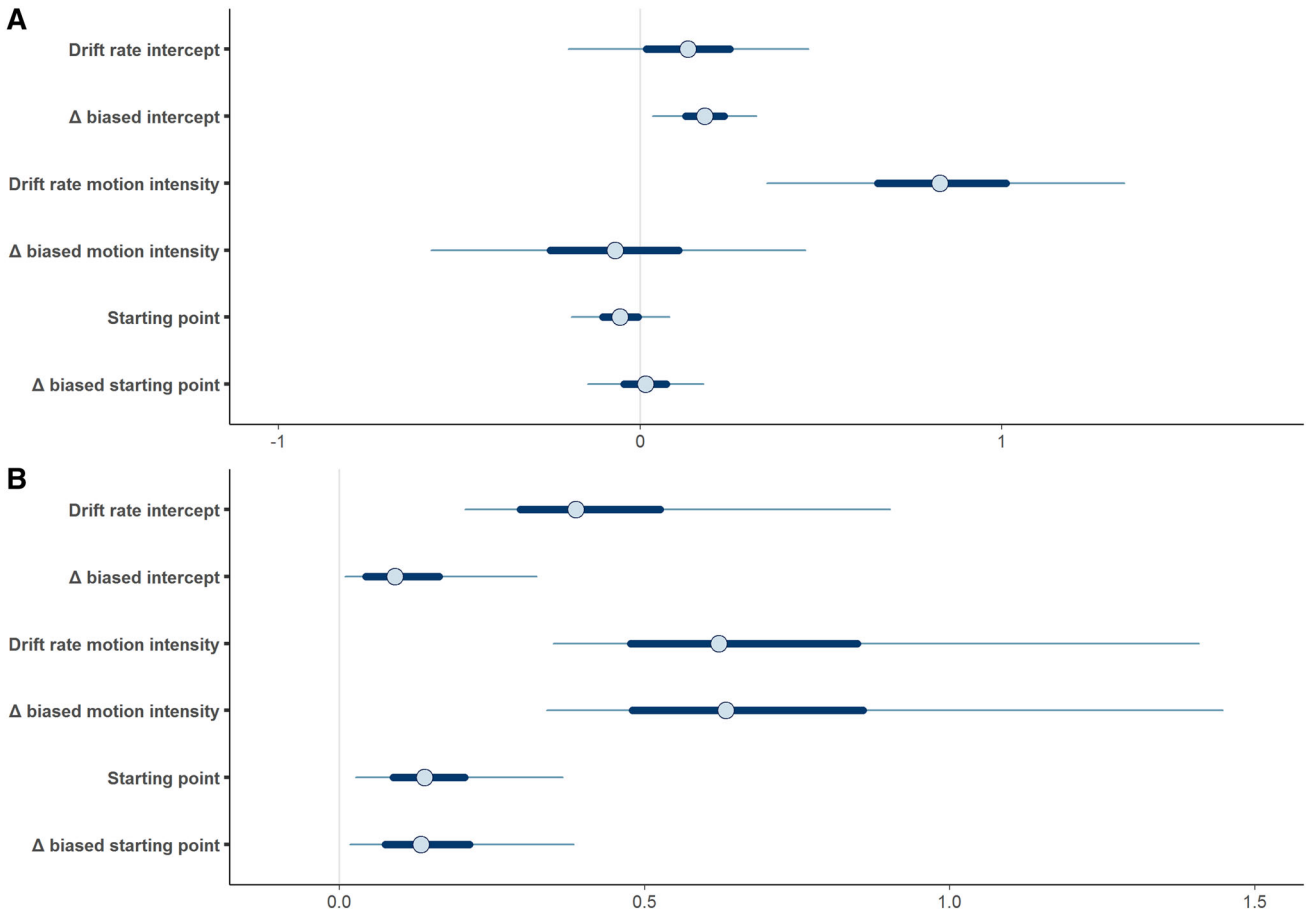

Fig. 2 Parameter estimates of partial pooling DDM fits. **a** Median, 50 and 95% credible regions of group-level parameter estimates for effects on the drift rate and the starting point. **b** Standard deviations of the random participant effects. Large standard deviation indicates large inter-individual differences between participants. Parameters: Drift rate intercept = Offset in the drift rate in the unbiased condition. Δ biased intercept = Additive effect of biased condition on the drift rate offset. Drift rate motion intensity = Effect of motion intensity on the drift rate in the unbiased condition. Δ biased motion intensity = Additive effect of biased condition on the effect of motion intensity on the drift rate. Starting point = Starting point for evidence accumulation in the unbiased condition. Δ biased starting point = Additive effect of biased condition on the starting point

Table 1 Drift diffusion parameter estimates

Parameter	Description
Drift rate intercept	Offset in the drift rate in the unbiased condition. This represents the tendency to accumulate evidence for a given motion direction, independently of motion intensity
Δ biased intercept	Additive effect of biased condition on the drift rate offset
Drift rate motion intensity	Effect of motion intensity on the drift rate in the unbiased condition. Higher motion intensities lead to a larger drift rate. This indicates how well the motion intensity is processed, and is roughly analogous to the sensitivity in the psychometric function
Δ biased motion intensity	Additive effect of biased condition on the effect of motion intensity on the drift rate. Negative values thus indicate decreased performance in the biased condition, whereas positive values indicate better performance
Starting point	Starting point for evidence accumulation in the unbiased condition. Positive values indicate that the starting point is shifted toward the upper boundary (rightward responses), whereas negative values indicate a shift toward the lower boundary
Δ biased starting point	Additive effect of biased condition on the starting point. Positive values indicate a shift toward the upper boundary, relative to the unbiased condition

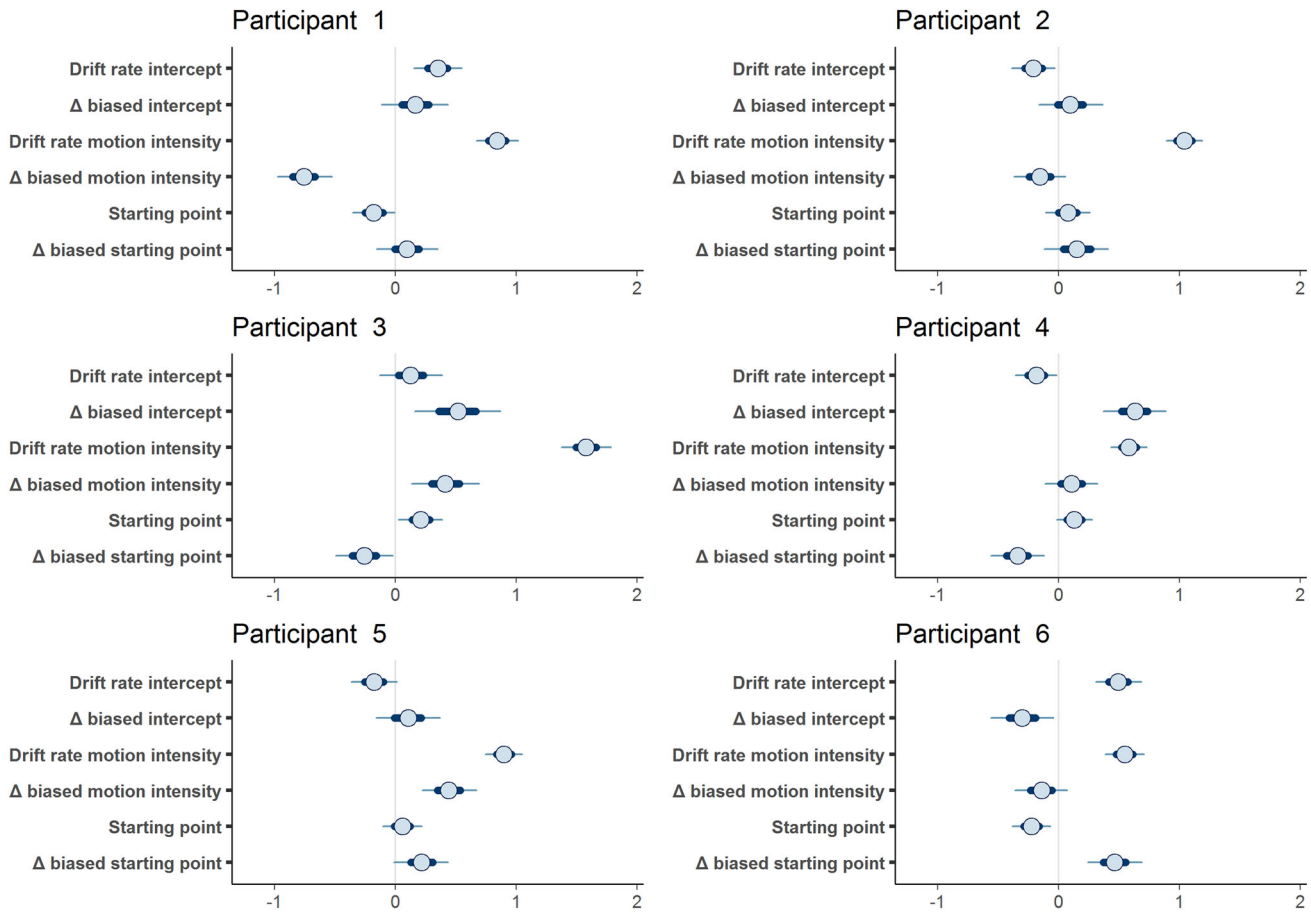

Fig. 3 Parameter estimates of individual DDM fits for every participant. Median, 50 and 95% credible regions of parameter estimates for effects of motion intensity and biased condition on the drift rate and starting point parameters for each subject individually. Parameters are the same as in Fig. 2A. There are differences in how participants incorporated a bias into their decision making (see main text for details)

participant 2, the model explains the biased responses as an increased starting point in the evidence accumulation process, indicated by the positive additive effect on the starting point parameter. The other participant to show an increased starting point is participant 5.

In summary, our results show that participants can incorporate a prior belief about motion direction into their decision-making process, and this results in a shift of the psychometric function without loss of sensitivity. In terms of the DDM, the prior belief manifests itself as either a change in starting point or drift rate. Participants adopt different strategies, resulting in different combinations of parameters of the drift diffusion model.

Discussion

Both behavioral data and modeling demonstrate the importance of considering prior beliefs in sensory processing of dynamic vestibular stimuli. In this study, we assessed the effect of prior beliefs about the relative probability of motion direction using a cognitive process model. A joint analysis of both choices and RTs allows the extraction of richer information than is available from analyzing either choices or RTs independently. While the application of cognitive process models has been used in other sensory modalities [16, 17], this is not true for vestibular sensory processing. In comparison with other sensory systems, however, the vestibular system is comparatively well understood in terms of the sensory dynamics, making it an ideal candidate for furthering our understanding of perceptual decision making and, in particular, cognitive effects on decision making. Recently, Merfeld and colleagues [2] discussed perceptual decision making in the context of Bayesian processing of dynamic sensory information, and proposed a high-pass filtering mechanism. Furthermore, detailed computational models of vestibular sensory processing exist [18, 19], and this will allow that the investigation of how decision making may be incorporated in Bayesian models of sensory inference. The

relationship between a Bayesian model of evidence accumulation and the drift diffusion model has been discussed elsewhere [20], and the authors point out that the two are equivalent under certain assumptions. As pointed out by Merfeld et al. [2], however, the standard drift diffusion model may be inappropriate for the type of evidence accumulation required for the real-time processing of dynamic sensory information.

In our study, we found that all participants incorporate the altered prior belief induced by verbal instructions into their perceptual decision-making process, albeit in different ways. In particular, the effects of an induced response bias can be seen in both an increased starting point and an altered drift rate. The former may represent a cognitive process that operates prior to, and possibly independently of perceptual processing, whereas the latter operates dynamically, during the evidence accumulation process. Future research needs to investigate to what extent the parameters of cognitive process models involved in perceptual decision making, such as changes in drift rate or starting point, can be mapped onto different underlying neural mechanisms. Further insight may be gained by combining cognitive process models with EEG recordings, allowing a more fine-grained distinction between processes operating prior to stimulus presentation and processes operating during the accumulation of sensory evidence. Ellis and Mast [21] have previously argued that the vestibular system is well suited for investigating the connection between cognition and perception, and we claim that vestibular decision making represents a particularly promising paradigm for future research.

Compliance with ethical standards

Conflicts of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethical standards All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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