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Abstract:	Objective: Vestibular cognition is a growing about the underlying mechanisms. Methods: We tested the effect of prior belief 80:20) of motion direction (yaw rotation) usin analyzed choices individually with a logistic response times using a cognitive process m Results: The results show that self-motion p to a shift of the psychometric function, witho diffusion analysis showed that at the group b offset to the drift criterion. However, individu in how they use cognitive information in per- level, the response bias induced by a prior b point (prior to evidence accumulation) or drift Conclusions: Participants incorporate prior b albeit in different ways.	field of interest and relatively little is known is about the relative probability (50:50 vs. ing a direction discrimination task. We regression model and together with nodel. herception is altered by prior belief, leading but a loss of sensitivity. Hierarchical drift level, prior belief manifests itself as an hal model fits revealed that participants vary ceptual decision-making. At the individual belief resulted either in a change in starting ft rate (during evidence accumulation). belief in a self-motion discrimination task,
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Author Comments:	Dear Editor We hereby submit a manuscript entitled "Vestibular Cognition: The Effect of Prior Belief on Vestibular Perceptual Decision-Making", written by myself (first author), Manuel Klaus and Fred Mast (senior author). The research in this manuscript is new, has not been submitted elsewhere, nor is it currently under review in another journal. It shows how vestibular self-motion perception can be altered by prior belief, and we used sophisticated data analyses, including drift diffusion models, to analyze the data. The findings are an important contribution to a better understanding of vestibular cognition. We thank you for considering our manuscript. Yours sincerely,
<i>F</i>	Andrew Ellis, Manuel Klaus und Fred Mast

Vestibular Cognition: The Effect of Prior Belief on Vestibular Perceptual Decision-Making

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Abstract

Objective: Vestibular cognition is a growing field of interest and relatively little is known about the underlying mechanisms.

Methods: 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*.

Results: 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).

Conclusions: Participants incorporate prior belief in a self-motion discrimination task, albeit in different ways.

Conflict of interest statement: 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.

Keywords: vestibular cognition, anticipation, bias, direction recognition, drift diffusion model, expectation, perceptual decision-making

Word count: 2642

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 are prior beliefs. In order 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) in order 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 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].

52 The goal of this study is to investigate whether and how prior belief exerts an effect on

53 passive whole body motion discrimination, similar to that found in other sensory modalities.

54 Specifically, the question is whether participants can introduce a bias by changing their

55 response criterion, and if so, which cognitive processes are involved. In order to achieve this

56 goal, we analyzed choices using a multi-level logistic regression model, and jointly analyzed

57 choices and RTs using a hierarchical drift diffusion model, in a simple direction

58 discrimination task.

59 Methods

60 Subjects

61 Six healthy volunteers (3 female/3 male, aged between 22 to 29) took part in this study.

Informed consent was obtained from all participants. Ethical approval was obtained from theEthics Committee of the University of Bern.

64 Motion Stimuli

Motion stimuli were generated using a 6 degree of freedom motion platform (6DOF2000E, MOOG Inc., East Aurora, NY). We used single cycle sinusoidal acceleration motion profiles with a frequency of 1Hz. 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.

71 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. In order 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.

82 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.

89 Data Analysis

Participants' choices were analyzed using a Bayesian hierarchical logistic regression model
 incorporating two additional parameters in order to account for attentional lapses and guesses

92 [11]. We quantified a response bias as an additive effect of the biased condition on the
93 parameter of the linear predictor. Choices and RTs were then jointly analyzed using a
94 Bayesian hierarchical drift diffusion model [12]. All models were estimated using the brms
95 [13] and rstan [14] R packages. We estimated several models allowing for an effect of
96 response bias on the DDM parameters, and selected the best model based on the leave-one97 out cross validation (LOO) method [15].

⁹₁₀ 98 **Results**

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99 Probability of Rightward Responses

13 14 100 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 15 101 16 102 for rightward motion, and negative for leftward motion. The scale represents the standardized 17 103 peak velocity. Verbal instructions led to an overall increase in the proportion of rightward 18 19 104 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 20 105 21 106 responses at the expense of the ability to successfully discriminate between left and right; the 22 107 probability of giving a rightward response is high even for trials with high leftward velocity. 23 108 It is noteworthy that performance of this participant in the unbiased condition is absolutely 24 25 109 comparable to the other participants.

26 27 110 Figure 1B shows the group-level parameter estimates of the logistic fit. The fixed effect for 28 111 the intercept in the unbiased condition (unbiased crit) reveals that participants did not favor ²⁹ 112 either of the directions, and the fixed effect of motion intensity (sensitivity) shows that 30 113 stronger motion intensity increased the probability of giving a rightward response. The third 31 32 114 and fourth parameters represent additive effects for the intercept (Δ biased crit) and slope of 33 115 motion intensity (Δ biased sensitivity) in the biased condition. The additive effect on the ³⁴ 116 intercept represents a shift of the psychometric curve along the x-axis, shown in Figure 1C. 35 The fact that the 95% credible region lies to the right of zero means that in the biased 117 36 37 118 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 38 119 39 120 centered at zero means that on average, participants' altered decision criterion was not ⁴⁰ 121 accompanied by a loss of sensitivity, resulting in similarly shaped curves in Figure 1C. 41 ¹¹₄₂ 122 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 43 123 44 124 losing the ability to discriminate between motion directions.

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 48 126 FIGURE 1 ABOUT HERE
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50 127 Figure 1: Response data and hierarchical logistic regression model

51 52 128 (A) Proportion of rightward responses as a function of standardised motion intensity in biased ⁵³ 129 and unbiased condition for all participants. (B) Median, 50% and 95% credible regions of 54 130 group-level parameter estimates for the logistic fit. (C) Estimated psychometric curves for 55 56 131 biased and unbiased condition at group level. Parameters: Unbiased crit = intercept for the 57 132 unbiased condition. Sensitivity = slope parameter for the unbiased condition. Δ biased crit = 58 133 additive effect on intercept for biased condition. Δ biased sensitivity = Additive effect on 59 134 sensitivity for biased condition.

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2 136 Drift Diffusion Analysis

We next assessed whether the criterion shift shown in Figure 1 was due to a shifted starting 4 137 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 9 141 a change in both starting point and drift rate as a function of instruction conditions. 10 142 Additionally, 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. 14 145 These models were not distinguishable based on LOO. We therefore report parameter 15 146 16 147 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. 20 150

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24152Table 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.

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² 154 FIGURE 2 ABOUT HERE

155 Figure 2: Parameter estimates of partial pooling DDM fits

5 (A) Median, 50% and 95% credible regions of group-level parameter estimates for effects on 156 6 7 the drift rate and the starting point. (B) Standard deviations of the random participant effects. 157 8 158 Large standard deviation indicate large inter-individual differences between participants. 9 159 Parameters: Drift rate intercept = Offset in the drift rate in the unbiased condition. Δ biased 10 intercept = Additive effect of biased condition on the drift rate offset. Drift rate motion 11 160 12 161 intensity = Effect of motion intensity on the drift rate in the unbiased condition. Δ biased 13 motion intensity = Additive effect of biased condition on the effect of motion intensity on the 162 14 drift rate. Starting point = Starting point for evidence accumulation in the unbiased condition. 163 15 Δ biased starting point = Additive effect of biased condition on the starting point. 16 164

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21 The intercept for the drift rate in the unbiased condition in Figure 2A is slightly above zero, 22 167 23 indicating a slightly increased probability of reaching the upper boundary. This parameter 168 24 represents the amount of evidence that is accumulated independently of the motion intensity; 169 25 the effect of this becomes important at low motion intensities. The additive effect on this 170 26 intercept in the biased condition is greater than zero, with the 95% credible region excluding 27 171 28 172 0; this means that, at the group level, participants' drift rates for rightward motion were 29 173 increased due to the instruction favoring one direction of motion. The effect of motion 30 174 intensity is positive, indicating that participants incorporated information about the stimulus 31 into their drift rates. Notably, the fixed additive effect of the biased condition on the motion 175 32 intensity parameter is effectively zero. Therefore, at the group-level, the biased condition 33 176 34 177 does not result in altered processing of motion intensity. The starting point in the unbiased 35 178 condition is zero; participants did not favor either motion direction prior to evidence 36 accumulation. The additive effect in the biased condition is also zero, meaning that, on 179 37 38 180 average, the biased condition did not result in an altered starting point.

39 Figure 2B shows the standard deviations of the random participant effects. Large standard 40 181 deviation mean that there were large inter-individual differences between participants. While 41 182 42 183 the standard deviation of the additive effect on the intercept in the biased condition is 43 184 relatively small, indicating that this effect is consistently found across all participants, Figure 44 2B reveals that there is considerable variability between participants for both the slope of 185 45 motion intensity in the unbiased condition and the additive effect on the slope in the biased 46 186 47 187 condition. Since the additive effect on the slope is centered at zero, a large standard deviation 48 188 indicates that there are positive and negative effects at the individual level. Any effects at the 49 189 individual level may cancel out. Therefore, we report parameter estimates for each participant 50 190 individually. The results are shown in Figure 3. 51

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195 FIGURE 3 ABOUT HERE

Figure 3: Parameter estimates of individual DDM fits for every participant 196

4 197 Median, 50% and 95% credible regions of parameter estimates for effects of motion intensity

198 and biased condition on the drift rate and starting point parameters for each subject

199 individually. Parameters are the same as in Figure 2A. There are differences in how

200 participants incorporated a bias into their decision-making (see main text for details).

14 203 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 15 204 16 205 condition, resulting in a small cumulative effect of motion intensity in the biased condition, 206 this participant does not seem to incorporate information about motion direction into the 19 207 decision-making process; 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 20 208 21 209 offset is not visible in the unbiased condition, as the participant takes the motion intensity ²² 210 into account. A similar decrease in stimulus processing is visible in participant 2. The 211 response bias in this participant is explained by an altered starting point in the biased 25 212 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 26 213 27 214 the motion intensity. This results both in more efficient evidence accumulation for large 215 motion intensities and a biased drift criterion toward rightward responses. Finally, participant ₃₀ 216 6 shows no effect on stimulus processing, and a decreased offset in the drift rate in the biased 31 217 condition. Similarly to participant 2, the model explains the biased responses as an increased 32 218 starting point in the evidence accumulation process, indicated by the positive additive effect ³³ 219 on the starting point parameter. The other participant to show an increased starting point is 220 participant 5.

221 In summary, our results show that participants can incorporate a prior belief about motion 38 222 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 39 223 40 224 either a change in starting point or drift rate. Participants adopt different strategies, resulting 225 in different combinations of parameters of the drift diffusion model.

Discussion 45 226

⁴⁶ 227 Both behavioral data and modeling demonstrates the importance of considering prior beliefs 228 in sensory processing of dynamic vestibular stimuli. In this study, we assessed the effect of 49 229 prior beliefs about the relative probability of motion direction using a cognitive process 50 230 model. A joint analysis of both choices and RTs allows the extraction of richer information 51 231 than is available from analyzing either choices or RTs independently. While the application ⁵² 232 of cognitive process models has been used in other sensory modalities [16, 17], this is not 53 true for vestibular sensory processing. In comparison to other sensory systems, however, the 233 54 55 234 vestibular system is comparatively well-understood in terms of the sensory dynamics, making 56 235 it an ideal candidate for furthering our understanding of perceptual decision-making, and in 57 236 particular, cognitive effects on decision-making. Recently, Merfeld and colleagues [2] 58 237 discussed perceptual decision making in the context of Bayesian processing of dynamic 59 60 238 sensory information, and proposed a high-pass filtering mechanism. Furthermore, detailed 61

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1 2 3 4 5 6 7 8	239 240 241 242 243 244 245	comp invest infere diffus equiv howe	utational models of vestibular sensory processing exist [18, 19], and this will allow the igation of how decision-making may be incorporated in Bayesian models of sensory nce. The relationship between a Bayesian model of evidence accumulation and the drift ion model has been discussed elsewhere [20], and the authors point out that the two are alent under certain assumptions. As pointed out by Merfeld and colleagues [2], ver, the standard drift diffusion model may be inappropriate for the type of evidence nulation required for the real-time processing of dynamic sensory information.
9 10 11 12 13 14 15 16 17 18 19 20 21	246 247 248 249 250 251 252 253 254	In our verbal partic point prior dynan to wh makir under	e study, we found that all participants incorporate the altered prior belief induced by I instructions, into their perceptual decision-making process, albeit in different ways. In ular, the effects of an induced response bias can be seen in both an increased starting and an altered drift rate. The former may represent a cognitive process that operates to, and possibly independently of perceptual processing, whereas the latter operates nically, during the evidence accumulation process. Future research needs to investigate at extent the parameters of cognitive process models involved in perceptual decision- ng, such as changes in drift rate or starting point, can be mapped onto different lying neural mechanisms.
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$\begin{array}{c} 26\\ 27\\ 28\\ 29\\ 30\\ 31\\ 32\\ 33\\ 4\\ 35\\ 36\\ 37\\ 38\\ 39\\ 40\\ 41\\ 42\\ 43\\ 44\\ 456\\ 47\\ 48\\ 9\\ 50\\ 51\\ 52\\ 54\\ 55\\ 56\\ 57\\ 56\\ 56\\ 57\\ 57\\ $	256 257 258	1.	Benson AJ, Hutt EC, Brown SF (1989) Thresholds for the perception of whole body angular movement about a vertical axis. Aviat Space Environ Med 60:205–213.
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