

31

32 **Figure 1: Olivo-cerebellar loops, and internal model computations for processing otolith signals. A:**
 33 *Neural pathways and information processing in olivo-cerebellar loops. Sensory inputs and efference*
 34 *copies reach the cerebellum through mossy fibers and are processed in the granular layer. Granule cells*
 35 *convey this information to PCs through parallel fibers. PCs are anatomically clustered in microzones,*
 36 *and several microzones participating to a single olivo-cerebellar loop form a microcomplex. Further*
 37 *pathways exist in the vestibular circuitry: primary afferents also reach the vestibular nuclei, which*
 38 *project to the granular layer, and PCs may project collaterals to the granular layer. B: Ambiguity of the*
 39 *otolith organs. The otolith organs are analogous to a pendulum, whose position is sensed in egocentric*
 40 *head coordinates. Rightward head tilt or leftward acceleration cause a rightward deviation of the*
 41 *pendulum relative to the head, resulting in an identical activation of the otoliths. C: Mathematical*
 42 *formulation of the ambiguity. The otoliths sense the gravito-inertial acceleration (GIA), expressed as*
 43 *$GIA = G + A$ where G is the gravity vector and A a vector opposite to the linear acceleration (this*
 44 *convention is chosen for clarity purposes). The brain may resolve the ambiguity by tracking G , and*
 45 *computing A by subtraction ($A = GIA - G$). D: Internal model computations for otolith information*
 46 *processing. See text for description.*

47 Cerebellar computations are implemented by olivo-cerebellar loops (Fig. 1A) (Apps et al., 2018; Apps
 48 & Garwicz, 2005; Chaumont et al., 2013; De Zeeuw et al., 2011; Ozden et al., 2009; Sugihara & Quay,
 49 2007), within which a group of Purkinje Cells (PCs) in the cerebellar cortex project simple spikes (SS)
 50 to a group of cells in the cerebellum's output nuclei (the deep cerebellar nuclei, DCN, and vestibular
 51 nuclei, VN). These nuclei project throughout the nervous system to control behaviour, and to a group
 52 of Inferior Olive (IO) neurons that projects back to the cerebellar cortex. IO neuron influence on PCs
 53 induces Complex Spikes (CS) that act as teaching signals to drive cerebellar learning (Herzfeld et al.,
 54 2018; Kimpo et al., 2014; Lisberger, 1988; Nguyen-Vu et al., 2013). PCs within an olivo-cerebellar loop
 55 are anatomically clustered in sagittally oriented microzones of several hundred microns in length and

56 tenths of microns in width (Kostadinov et al., 2019; Ozden et al., 2009; Valera et al., 2016). An olivo-
57 cerebellar loop can be formed by multiple microzones that receive similar projections from the IO,
58 and collectively form a multizonal microcomplex (Apps & Garwicz, 2005; Cerminara et al., 2020) : in
59 this study we will use the term ‘microcomplex’ to refer to a set of PCs receiving identical IO projections,
60 and ‘loop’ to refer to the network of cortical, nuclear and IO neurons communicating with a
61 microcomplex.

62 Studies to date have pioneered the ‘microcomplex’ as a fundamental unit of cerebellar computation,
63 e.g. during saccadic eye movements (Herzfeld et al., 2015, 2018), tactile reflexes (Apps & Garwicz,
64 2005; Cerminara et al., 2020; Ekerot et al., 1991; Garwicz et al., 1998) or cognitive tasks (Kostadinov
65 et al., 2019). This has led to the notion that identifying PCs that receive identical IO inputs (i.e.
66 participate in the same microcomplex) allows parsing the cerebellar cortex into elementary
67 computation units (Herzfeld et al., 2015, 2018; Shadmehr, 2020). However, how to map such multi-
68 variable computations onto olivo-cerebellar loops raises fundamental questions. One possibility is that
69 each variable is represented by a different microcomplex such that multivariable computations are
70 implemented by parallel loops, each computing one variable. Alternatively, it is also possible that PCs
71 encoding fundamentally distinct variables may exist in a single microcomplex. Such a finding would
72 depart from the traditional view where one loop computes one variable and suggest that individual
73 microcomplexes can perform sequences of operations: Functionally distinct PCs perform distinct
74 computations using common teaching signals.

75 To distinguish between these two hypotheses we take advantage of a multivariable cerebellar
76 computation based on an internal model of self-motion, already widely studied in the literature (**Fig.**
77 **1B-D**) (Borah et al., 1988; Bos & Bles, 2002; Glasauer & Merfeld, 1997; Karmali & Merfeld, 2012;
78 Laurens & Angelaki, 2011, 2017; Laurens & Droulez, 2007; Merfeld, 1995; Oman, 1982; Ormsby &
79 Young, 1977; Zupan et al., 2002). A unique advantage of this system is the ability to map complex, but
80 well-understood, algorithmic computations implementing an internal model of the inner ear’s inertial
81 motion sensors, the otolith organs, into a cerebellar circuit that includes lobules X and IX of the
82 cerebellar vermis (Nodulus and Uvula; NU) (Laurens et al., 2013a, 2013b; Laurens & Angelaki, 2020;
83 Stay et al., 2019; Yakusheva et al., 2007, 2008, 2013).

84 Specifically, the otolith organs sense the sum of gravitational (G) and linear accelerations (A), which
85 are physically indistinguishable (Einstein, 1907), in head coordinates (**Fig. 1 B,C**). The otolithic signal is
86 therefore inherently ambiguous. Nevertheless, this ambiguity can be resolved by using additional
87 sensory information and motor inference copies to predict the two components of otolith activation,
88 gravity (G) and translational acceleration (A). On the one hand, the gravitational component G can be

89 predicted by tracking head rotation relative to gravity (**Fig. 1D**, green). A portion of the head's internal
90 model of motion (**Fig. 1D**, blue; not developed here for simplicity; (see (Karmali & Merfeld, 2012;
91 Laurens & Angelaki, 2011, 2017) for details), senses head rotation velocity (Ω) in an egocentric frame
92 of reference. The internal model converts Ω into allocentric velocity relative to gravity (block marked
93 '3D' in **Fig. 1D**), which is equivalent to the derivative of gravity in head coordinates (dG/dt). This signal
94 is integrated over time (block marked 'j' in **Fig. 1D**) to estimate the gravity vector in head coordinates
95 (G). On the other hand, head translation may be derived directly from motor efference copies during
96 active translation (**Fig. 1D**, violet, broken lines), but is unpredictable during passive movements.

97 Altogether, the internal model can predict otolith signals during active tilt and translations (based on
98 motor commands), or during passive tilt (based on rotation signals). Thus, otolith prediction errors
99 occur during passive translations, or if tilt signals are erroneous, which can occur because of sensory
100 noise or incorrect rotation signals from the canals. Since these tilt errors are generally smaller and
101 scarcer, the brain preferentially interprets otolith prediction errors as translation. Accordingly, otolith
102 prediction errors induce a perception of translation and the corresponding stabilizing eye movements,
103 irrespective of whether the prediction error originates from an actual translation or an artificially
104 generated incorrect canal signal (Angelaki et al., 1999; Hess & Angelaki, 1999; Khosravi-Hashemi et al.,
105 2019; Merfeld et al., 1999). Otolith prediction errors also trigger low-frequency feedback (**Fig 1D**,
106 violet) that gradually correct the underlying rotation signals and tilt estimates.

107 Based on SS responses exclusively, two populations of PCs were identified that perform distinct steps
108 in the internal model's computation. First, translation-selective cells (**Fig. 1Ds**) encode otolith
109 predictions error (Laurens et al., 2013a, 2013b; Laurens & Angelaki, 2020; Stay et al., 2019; Yakusheva
110 et al., 2007, 2008, 2013). These cells respond selectively to passive translation, indicating that they (i)
111 receive otolith inputs, (ii) are cancelled by tilt signals originating from rotation sensing (**Fig. 1D**;
112 Laurens et al., 2013b) and (iii) encode sensory prediction errors that result from artificial canal
113 stimulation (Laurens et al., 2013a). Critically, the responses of translation-selective cells in the VN and
114 DCN are attenuated during active head translations (Carriot et al., 2013; Mackrous et al., 2019), a
115 finding that confirms that the internal model uses efference copies to predict otolith signals.

116 Second, another PC type in the NU encodes tilt velocity (**Fig. 1D**, tilt-selective cells; (Hernández et al.,
117 2020; Laurens et al., 2013b; Laurens & Angelaki, 2020; Stay et al., 2019). These cells modulate more
118 during tilt than translation in phase to tilt velocity (Laurens & Angelaki, 2020). Importantly, 3D motion
119 stimuli have revealed that these cells encode transformed rotation signals (dG/dt), and not egocentric
120 rotation velocity (Ω) (Laurens et al., 2013b).

121 Despite a good understanding on the properties of SS responses, little is currently known about CSs,
122 which are fundamental for understanding the organisation of the corresponding cerebellar circuits.
123 Previous CS studies were limited to rotation stimuli (Barmack & Shojaku, 1995; Fushiki & Barmack,
124 1997; Kitama et al., 2014; Yakhnitsa & Barmack, 2006), or only characterized translation-selective cells
125 (Yakusheva et al., 2010). A crucial, yet unanswered, question is whether CS firing is different in tilt-
126 selective and translation-selective cells: this would imply that there are two distinct cerebellar loops.
127 Alternatively, if tilt-selective and translation-selective cells exhibit similar CS firing, they may comprise
128 a single loop using the same teaching signals.

129 Here, we analysed the CS firing of both tilt- and translation-selective cells during combinations of tilt
130 and translation stimuli, as well as 3D motion (Laurens et al., 2013a, 2013b). Surprisingly, we found
131 that the CS firing of both cell types is identical, and occurred specifically during translation. This
132 indicates that the teaching signal to both cell types is driven by otolith prediction error, which is the
133 output of the internal model implemented by the NU. We interpret these findings in the context of a
134 previously proposed learning rule (Dean et al., 2002, 2010; Dean & Porrill, 2014), and validate our
135 interpretation by simulating a neural network model that learns to discriminate tilt from translation.

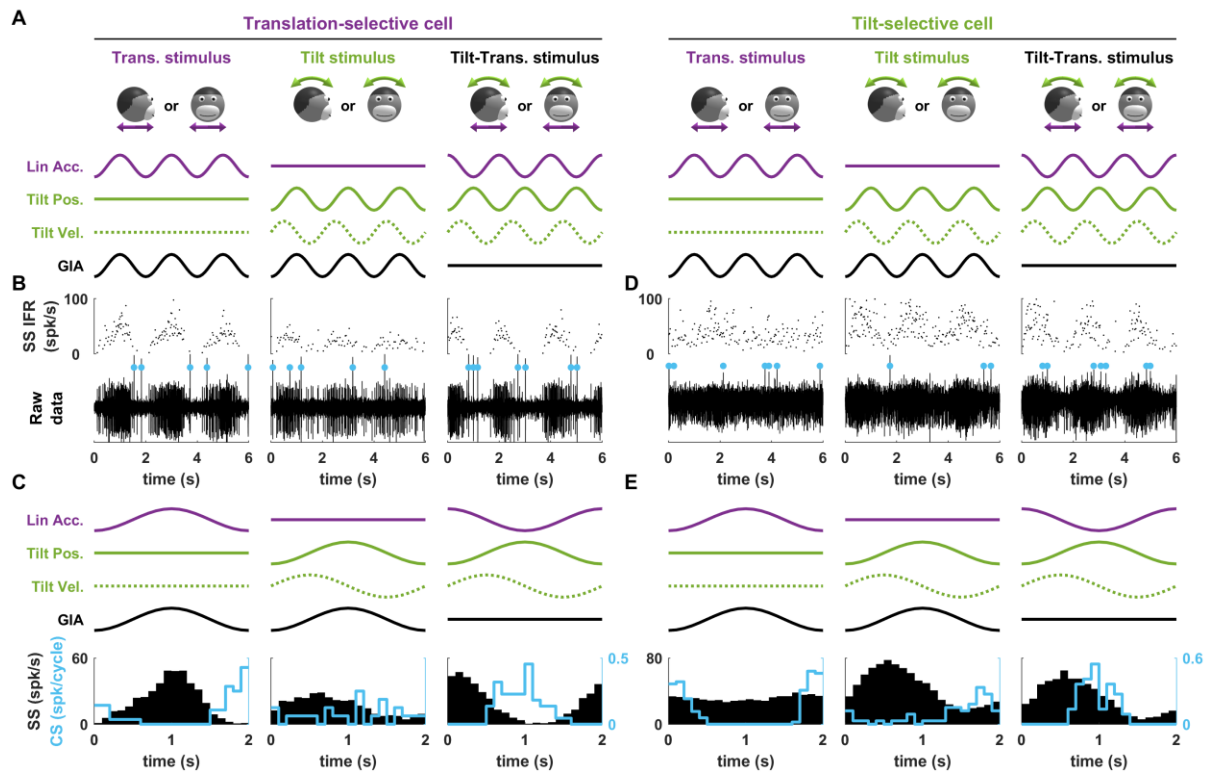
136 **Results**

137 We analysed CSs of 66 out of 211 Purkinje cells recorded in lobules IX-X of the cerebellar vermis
138 (Laurens et al., 2013a, 2013b) that could be identified consistently across trials and followed by a
139 pause in SS activity for at least 10 ms. Neurons were recorded during sinusoidal translation (**Fig. 2A**,
140 left) and tilt (**Fig. 2A**, middle) at 0.5 Hz (Angelaki et al., 1999, 2004; Laurens et al., 2013a, 2013b; Shaikh
141 et al., 2005; Yakusheva et al., 2007, 2008, 2013), which activated the otoliths identically (**Fig. 2A**, GIA).
142 A few cells were also recorded during: (1) out-of-phase tilt and translation (tilt-translation, **Fig. 2A**,
143 right), where linear acceleration and tilt cancel each other, such that the otoliths are not activated but
144 the canals sense velocity; and (2) in-phase tilt + translation (not represented in figures; see (Laurens
145 et al., 2013b; Laurens & Angelaki, 2016)). We used a spatio-temporal tuning model (Laurens et al.,
146 2013b; Laurens & Angelaki, 2016) together with a bootstrap test to classify cells as translation-
147 selective (larger response to translation), tilt-selective (larger response to tilt), GIA-selective (same
148 response to tilt and translation, similar to otolith afferents), composite (cells who could not be
149 classified in one of these categories) or non-responsive.

150 *Example cells*

151 Responses of example tilt- and translation-selective neurons are shown in **Fig. 2**. The translation-
152 selective cell (**Fig. 2B,C**) shows vigorous SS response during translation (**Fig. 2B,C**, left), but not during

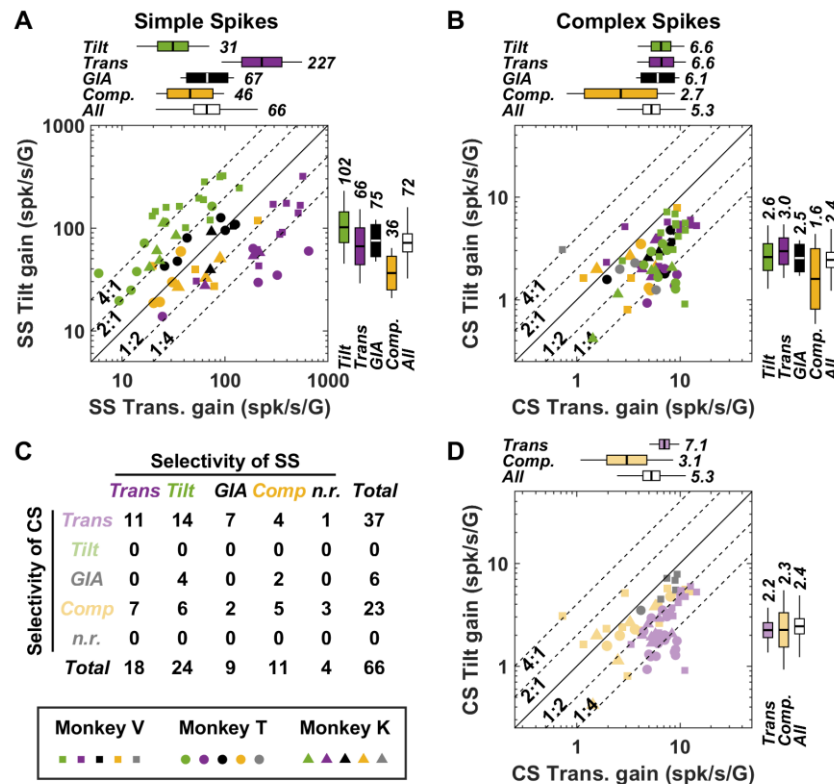
153 tilt (**Fig. 2B,C**, middle). During translation, the cell fired CSs during the trough of the SS response (**Fig.**
 154 **2B,C**, left, marked by cyan dots). In contrast, the phase-locked firing was weaker during tilt (**Fig. 2B,C**,
 155 middle). During tilt-translation (**Fig. 2B,C**, right), SSs and CSs maintained their phase relationship
 156 relative to the translational component of the stimulus, as expected if they were both driven by
 157 translation.



158 **Figure 2: Representative Purkinje cells during tilt/translation. A:** illustration of the motion stimuli.
 159 Violet and solid green curves: inertial acceleration and tilt position; the sum gives the GIA (black). Tilt
 160 velocity is indicated by broken green curves. **B:** Spiking activity of a translation-selective cell. Bottom
 161 traces show the raw extracellular voltage. CSs are marked by cyan dots. Upper traces show
 162 instantaneous firing rate (IFR) of the SSs. **C:** Average firing histograms of SSs (black) and CSs (cyan).
 163 **D,E:** Spiking activity and average firing of a representative tilt-selective cell (layout as in B,C).

165 The second example neuron (**Fig. 2D,E**) is representative of tilt-selective cells (Laurens et al., 2013b;
 166 Laurens & Angelaki, 2020; Stay et al., 2019): SS modulation was higher during tilt compared to
 167 translation (**Fig. 2D,E**, middle versus left). Consistently, groups of 2-3 CSs occurred at regular phases
 168 during each cycle of translation (**Fig. 2D**, left), such that a clear CS modulation occurred during
 169 translation (**Fig. 2E**, left). In contrast, CS modulation was weaker during tilt (**Fig. 2E**, middle). During
 170 tilt-translation (**Fig. 2D,E**, right), when SSs occurred during tilt (**Fig. 2E**, right versus middle), CS
 171 modulation maintained its phase with respect to the translational component of the stimulus. Thus,

172 this cell's CS firing (**Fig. 2E**) was locked to head translation, and conspicuously similar to that of the
 173 translation-selective cell (**Fig. 2C**).



174

175 **Figure 3: Response modulation and classification of the SS and CS firing across the population of PCs.**

176 **A:** Tilt versus translation response gain of SS firing. Cells are color-coded based on their classification
 177 (green, violet, black and yellow: tilt-, translation-, GIA-selective and composite). Marker shapes indicate
 178 the animal in which cells were recorded (see legend on lower left corner). The boxes and whisker plots
 179 represent geometrical average (box center), 95% confidence interval (box) and standard deviation
 180 (whiskers) of the gain for each cell type and all cells together (white). Broken black lines parallel to the
 181 diagonal represent the level at which tilt response gain is 4x, 2x, 1/2x and 1/4x the translation response
 182 gain. **B:** Tilt versus translation response gain of CS firing. Cells are color-coded based on their SS
 183 classification, i.e. as in A. **C:** Contingency matrix between the classification of SS and CS response
 184 sensitivity. **D:** Tilt versus translation response gain of CS firing, as in B, but with cells classified based
 185 on their CS response (green, violet, grey and yellow: tilt-, translation-, GIA-selective and composite).

186 SS and CS response gains

187 Consistent with previous studies (Laurens et al., 2013b, 2013b; Laurens & Angelaki, 2020; Stay et al.,
 188 2019), cells were classified based on their SS response gain to tilt and translation, computed along the
 189 preferred direction (PD) and expressed in identical units of spk/s/G. By definition, the gains of 18/62
 190 cells (29%) translation-selective cells appear below the diagonal (**Fig. 3A**, violet) since they respond

191 more to translation, spanning a range of 100 to 1000 spk/s/G. The gains of 24/62 (39%) tilt-selective
192 cells appear above the diagonal (**Fig. 3A**, green), spanning 20 to 300 spk/s/G during tilt, but orders of
193 magnitude smaller during translation. GIA-selective and composite cells (20/62, 32%) lie close to the
194 diagonal. These proportions and ranges of response gains resemble those reported by the broader
195 cell population (Laurens et al., 2013b), indicating that the cells analysed here are representative of the
196 full population. Furthermore, they are similar to the population responses of subsequent studies using
197 stimuli based on Gaussian (rather than sinusoidal) temporal profiles (Laurens & Angelaki, 2020) or
198 recorded in mice (Stay et al., 2019).

199 We next examined the modulation gain of CS. In **Fig. 3B**, neurons are color-coded based on the
200 selectivity of their SS response, i.e. as in **Fig. 3A**. Remarkably, most neurons, including all tilt-selective
201 cells (green), appeared below the diagonal. Thus, like the examples in **Fig. 2**, the CS modulation of
202 both translation- and tilt-selective cells was higher during translation than tilt. In fact, the average CS
203 modulation of tilt-, translation- and GIA-selective cells were identical during translation (6.6, 6.6 and
204 6.1 spk/s/G respectively, **Fig. 3B**, upper box plots; $p=0.79$, Kruskal-Wallis non-parametric ANOVA) and
205 also during tilt (2.6, 3 and 2.5 spk/s/G respectively, **Fig. 3B**, rightward box plots; $p=0.65$, Kruskal-Wallis
206 non-parametric ANOVA). CS response gains appeared weaker and more variable in composite cells
207 (**Fig. 3B**, yellow boxes) and in cells whose SS didn't exhibit a significant modulation (**Fig. 3B**, grey
208 markers).

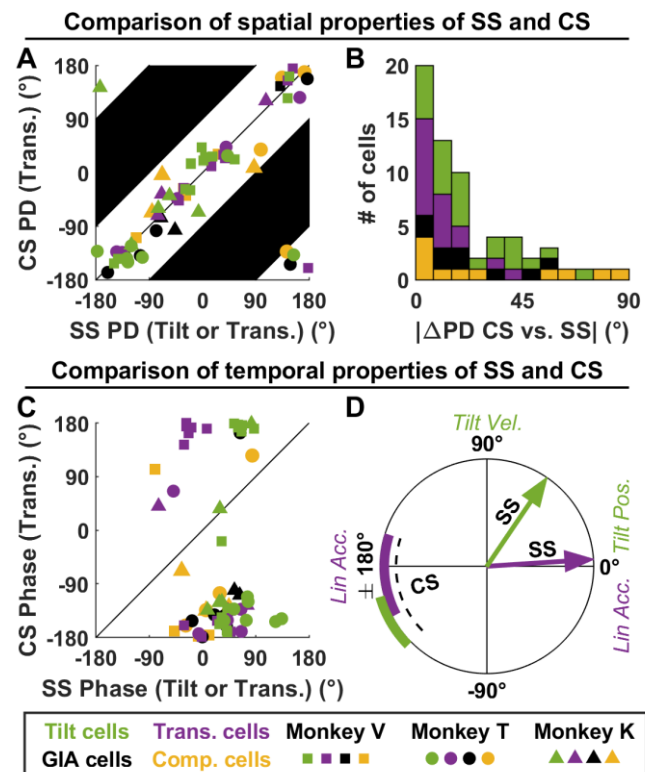
209 To evaluate whether CS modulation is significant on a cell-by-cell basis, we used the same classification
210 method used for SSs. We found that the majority of CS responses (37/66, 56%, **Fig. 3C**) was
211 independently classified as translation-selective, including most (14/24, 58%) cells that were classified
212 as tilt-selective based on their SSs. These cells appear in violet in **Fig. 3D**. CS modulation was similar
213 during tilt and translation in a few cells (6/66, 9%, **Fig. 3C**; grey markers in **Fig. 3D**). In the rest of the
214 population of cells (23/66, 35%), CS were classified as composite, indicating that they responded to
215 combinations of tilt and translation (**Fig. 3C**; yellow markers in **Fig. 3D**). Translation responses were
216 still larger than tilt responses in the majority (18/23) of these cells. Remarkably, no CS response was
217 classified as tilt-selective. This analysis confirms that CS are generally modulated during translation
218 and not during tilt, regardless of the selectivity of SS responses.

219 Spatio-temporal relationships of SS and CS firing

220 We next investigated whether SS and CS responses are spatially and temporally matched. All cells
221 were recorded along the forward-backward and lateral directions, allowing us to reconstruct the
222 neuron's tuning curve along all directions (see (Green et al., 2005; Laurens & Angelaki, 2016) for
223 details) and determine the direction along which its response is maximal (PD). These PD are

224 determined separately for SSs and CSs; and we test whether they are aligned in **Fig. 4A**. Note that SSs
 225 and CSs may occur along the same axis, but in anti-phase (e.g. as in **Fig. 2C**). In this case, it is equivalent
 226 to state that they have similar PD and opposite phase, or that they have similar phase and opposite
 227 PD. We adopt the former convention here: as a consequence, the difference in PD between SSs and
 228 CSs is never higher than 90° , and the corresponding area is blacked out in **Fig. 4A**. Note also that, since
 229 CSs are modulated during translation in tilt-selective cells, we compare the PD and phase of SSs during
 230 tilt to the PD and phase of CSs during translation in tilt-selective cells. For all other cell types, we
 231 compare SS and CS responses during translation. Note also that PDs are computed relative to the
 232 direction of the GIA, which is the stimulus activating the otoliths. For instance, a rightward tilt and
 233 leftward acceleration activate the otoliths in the same manner (**Fig. 1B**) and therefore correspond to
 234 the same PD.

235



236

237 **Figure 4: Spatio-temporal comparison of SS and CS responses.** **A:** Comparison of the PD of SSs (during
 238 tilt in tilt-selective cells and translation in other response groups) and CSs (during translation in all
 239 groups). Note that, by convention, the PD of SS and CS are never more than 90° apart (see text; the
 240 corresponding areas are marked in black). **B:** Histogram of the PD differences, measured as in A. **C:**
 241 Comparison of the response phase of SSs (during tilt in tilt-selective cells and translation in other
 242 response groups) and CSs (during translation in all groups) during motion along the PD (defined as in

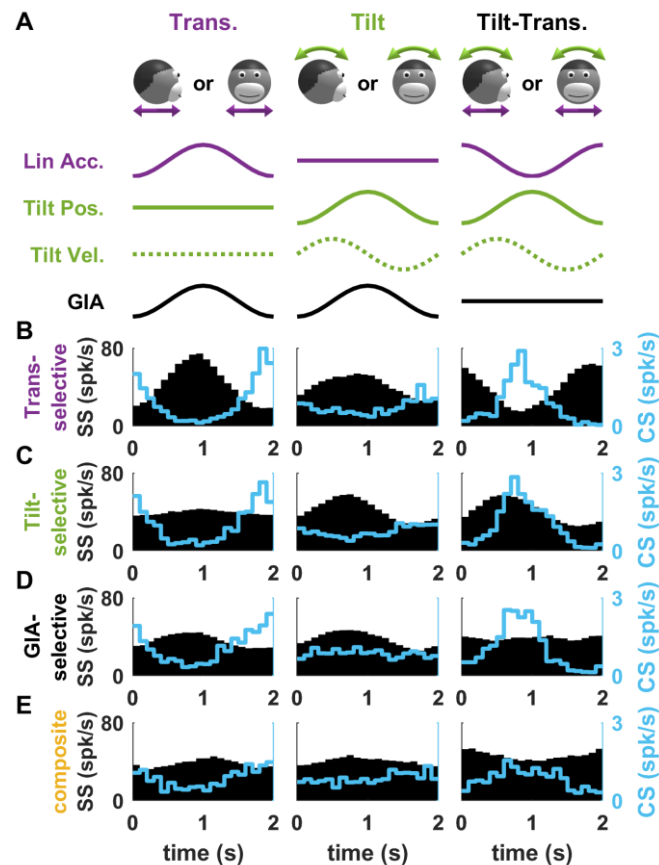
243 *A). D: Average response phase of SS (arrow) and CS (sectors representing confidence intervals) in tilt-*
244 *and translation-selective cells.*

245 We found that the spatial properties of SS and CS were closely aligned. Indeed, their PDs clustered
246 tightly along the diagonal in **Fig. 4A**. To measure how closely the PDs of SSs and CSs align, we computed
247 the absolute difference between them (**Fig. 4B**): this difference can range between 0° (when PDs are
248 aligned) and 90° (when they are orthogonal), and would be distributed uniformly if the PDs of SSs and
249 CSs were independent. We found that this difference was concentrated close to 0° (**Fig. 4B**; median:
250 14°, [10 19] CI; Kolmogorov-Smirnov test against uniform distribution: $p < 10^{-10}$), which confirm that the
251 PDs of SSs and CSs typically align closely.

252 We next examined the response phase of SSs and CSs. In line with our findings in (Laurens et al., 2013b;
253 Laurens & Angelaki, 2020), the SS response phase of translation-selective cells was close to peak
254 acceleration (**Fig. 4C**, violet; **Fig. 4D**, violet arrow), and that of tilt-selective cells was close to tilt
255 velocity (**Fig. 4C**, green; **Fig. 4D**, green arrow). In contrast, we found that the CS response phase during
256 translation clustered tightly close to -180° in both translation-selective cells (**Fig. 4C,D**; mean: -175°, [-
257 198 -152] CI) and tilt-selective cells (**Fig. 4C,D**; mean: -154°, [-173 -135] CI). This confirms that the CS
258 response of the entire population is homogenous in term of response phase, and identical in tilt- and
259 translation-selective cells.

260 *The tilt/translation discrimination microcomplex*

261 Previous studies (Herzfeld et al., 2015; Shadmehr, 2020) have proposed that groups of PCs within a
262 microcomplex, i.e. group of PCs that receive similar IO inputs, form a unit of cerebellar computation.
263 Our results indicate that microcomplexes in the NU are formed by mixtures of tilt-, translation-, GIA-
264 selective and composite PCs. In the next analysis, we pooled our data to compute CS and SS responses
265 of average PCs within a NU microcomplex.

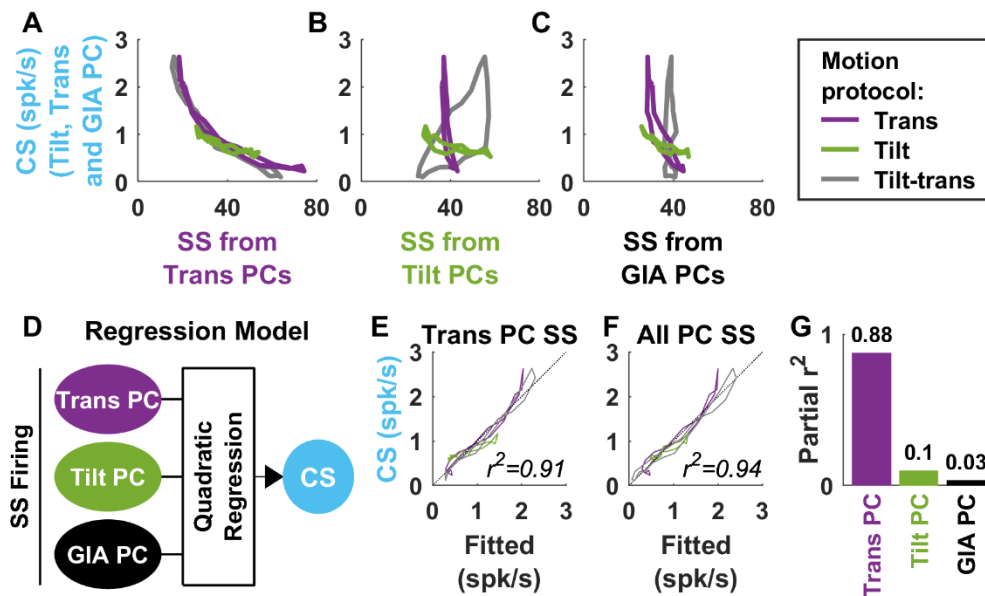


266

267 **Figure 5: Average SS and CS firing histograms of PCs belonging to a common microcomplex. A:**
 268 *Illustration of the motion stimuli and variables. B-E: Firing histograms of PCs belonging to all response*
 269 *groups. Black histograms: SS firing. Blue histograms: CS firing.*

270

271 To do so, we computed the PD of each cell's CS, and computed the SS and CS firing histograms across
 272 all trials collected within $\pm 45^\circ$ of the PD. This allowed us to 'spatially align' the firing of PCs with various
 273 PDs and to average their CS and SS responses. In agreement with **Fig. 3, 4**, we found that the CS
 274 response profile of translation-, tilt- and GIA-selective cells are highly similar (**Fig. 5B-D**, cyan).
 275 Furthermore, the combined SS activity of translation-selective PCs followed the response pattern of a
 276 translation-selective PC (**Fig. 5B**, black; compare e.g. with **Fig. 2C**). This indicates that translation-
 277 selective PCs that share similar IO inputs (and thus participate to a common microcomplex), also have
 278 similar SS firing, such that the population as a whole can be seen as a single translation-selective PC,
 279 a concept that has been described as 'super-PC' (Apps et al., 2018). Likewise, the population response
 280 of tilt-selective PCs (**Fig. 5C**) is representative of a single 'super' tilt-selective PC. In contrast, the SS
 281 response modulation of GIA-selective and composite cells was modest, indicating that these groups
 282 may not form coherent populations.



283

284 **Figure 5S1: CS firing can be predicted based on SS from translation-selective cells.** A-C: CS response
 285 (from Fig. 5B-D; averaged across tilt-, translation- and GIA-selective PCs) versus SS response of
 286 translation-selective (A), tilt-selective (B) and GIA-selective PCs (from Fig. 5B). There is a clear inverse
 287 relationship between CS and the SS from translation-selective cells (A). Importantly, this relationship
 288 holds across all motion protocols, including tilt (green). In contrast, there is no consistent relation
 289 between the average CS and the average SS responses of tilt- and GIA-selective cells. Therefore, CS
 290 firing is predicted based on the SS firing of translation-selective cells only. D: To test this, and
 291 investigate the SS of tilt- of GIA-selective cells can make any significant contribution to predicting CS
 292 firing, we performed a multiple regression analysis where SSs are the predictors and CS the dependent
 293 variable. We used a quadratic regression to account for the curvature of the curves in A. E,F: Relation
 294 between fitted (abscissae) and measured (ordinate) CS firing when the regression uses the SSs of
 295 translation-selective cells (E) or of all cells (F) as a predictor. The high r^2 score in (E) indicates that SS
 296 from translation-selective cells explain CS firing accurately, and increases only marginally in (F),
 297 indicating and SS from other cell types contributes little. G: Partial correlation analysis: based on the
 298 same rationale as panels E-F, each variable's partial r^2 reflects how much adding this variable to the
 299 others increase the regression's overall r^2 . The partial r^2 of SSs from translation-selective PC is high and
 300 significant ($p < 10^{-3}$, shuffling test), whereas the partial r^2 of SSs from other cell types is not significantly
 301 higher than expected by chance ($p = 0.064$ and $p = 0.41$). Thus, from a statistical point of view, the SSs of
 302 tilt- and GIA-selective cells don't contribute significantly to predicting CS firing.

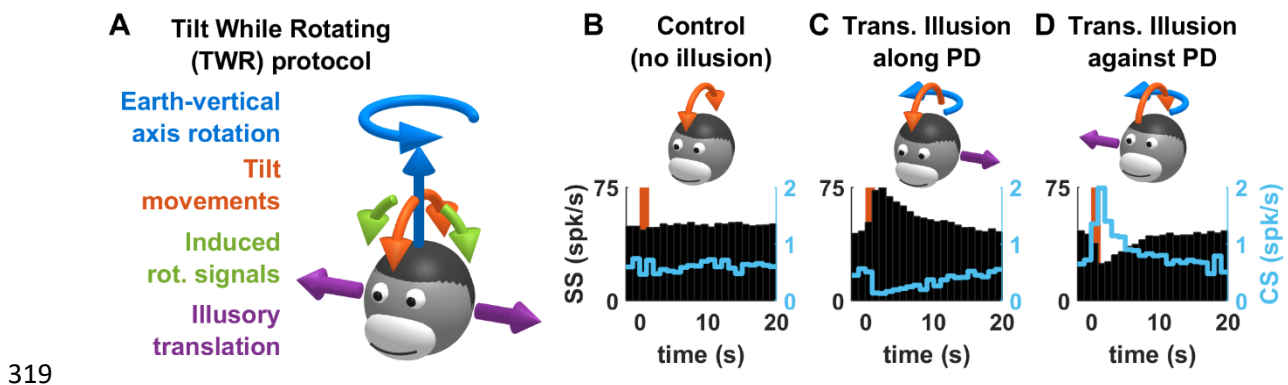
303 PCs project indirectly to the IO (Fig. 1A), and therefore their SS output may take part in controlling IO
 304 activity. We performed a regression analysis to evaluate the extent to which CS activity correlates with
 305 SS from different groups of PCs. In most cell groups (translation-, tilt- and GIA-selective PCs), CSs occur

306 predominantly during translation, and correlate with the SS firing of translation-selective cells. As CSs
307 and translation-selective cells also modulate to a limited extent during tilt (**Fig. 5B**), it is possible that
308 translation-selective cells alone can predict IO modulation. Indeed, a multiple regression analysis
309 between SS and CS firing (**Fig. 5D**) using a quadratic model to account for the curvature of the curves
310 in **Fig. 5A** demonstrated that the SS activity of translation-selective PCs predicts CS modulation during
311 both translation and tilt, and that adding the SS activity of tilt-selective cells as predictors didn't
312 improve the fitting significantly (**Fig. 5E-G**).

313 Thus, in summary, the data in **Fig. 5** offers a synthetic overview of a cell population which putatively
314 constitute a unit of computation in the NU. We will explore the possible architecture of such a circuit
315 further using modelling. But first we will further emphasize the experimental findings by examining CS
316 responses during 3D motion protocols used in (Laurens et al., 2013a, 2013b).

317

318 Three-dimensional responses and motion illusions

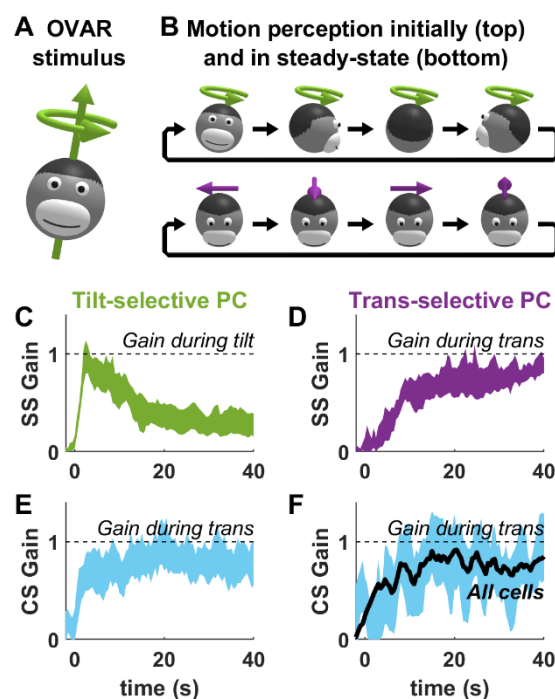


320 **Figure 6: SS and CS responses of translation-selective cells induced by Tilt While Rotating. A:**
321 *Rationale of the protocol (see text for details). B-D: SS (black) and CS (cyan) responses during control*
322 *tilt (B) or TWR inducing illusory translation along (C) or opposite (D) to the SS PD.*

323 We first analysed CS responses of PCs during Tilt While Rotating (TWR; **Fig. 6**; see (Laurens et al.,
324 2013a) for details). TWR consists of alternating tilt (i.e. forward/backward as illustrated in **Fig. 6A**,
325 orange arrows) superimposed on a constant-velocity yaw rotation (**Fig. 6A**, blue arrow). Due to the
326 physical properties of the semi-circular canals, these movements induce an additional rotation signal
327 in a direction orthogonal to the actual tilt (**Fig. 6A**, green arrows). Thus, from a sensory perspective,
328 TWR induces a sideward rotation signal, but without the corresponding activation of the otoliths since
329 the head is in fact immobile in this direction. The only coherent interpretation is that the head
330 undergoes a motion similar to a tilt-translation stimulus (**Fig. 2, 5**) where it tilts and translates
331 simultaneously. Accordingly, TWR induces an illusion of translation (sideward, **Fig. 6A**, violet). In

332 (Laurens et al., 2013a), we demonstrated that the SS firing of translation-selective PCs increases or
333 decreases when TWR induces illusory translation along or opposite to their PD.

334 We analysed the CS firing of a subset of 9 translation-selective cells in which CSs could be reliably
335 identified. As reported previously (Laurens et al., 2013a), there is no SS modulation when the tilt
336 movement occurred in the absence of yaw rotation (**Fig. 6B**, black). In contrast, there is a strong SS
337 firing increase/decrease when the simultaneous TWR stimulation induced illusory translation
338 along/opposite the cells' PD (**Fig. 6C,D**, black). The modulation of CSs followed a reciprocal pattern
339 (**Fig. 6C,D**, cyan), such that CSs increased when TWR induced an illusory translation opposite to the
340 cell's PD. Thus, similar to SS, CS responses are identical during real or illusory motion of the head.



341

342 **Figure 7: CS responses during OVAR. A,B:** Rationale of the OVAR protocol. The head rotates at a
343 constant velocity around a tilted axis. Initially (B, top), the motion is perceived veridically. However,
344 rotation signals from the semicircular canals fade out in about 20 s, resulting in a steady-state of an
345 illusion of translation (B, bottom). **C,D:** SS modulation gain of tilt- (C) and translation- (D) selective
346 cells, expressed relative to a tilt stimulus (as in panel B, top) for tilt-selective cells or a translation
347 stimulus (as in panel B, bottom) for translation-selective cells. The bands represent the 95% confidence
348 interval around the mean value. **E,F:** Cyan: CS modulation gain of tilt- (E) and translation- (F) selective
349 cells, expressed relative to a translation stimulus (as in panel B, bottom). The bands represent the 95%
350 confidence interval around the mean value. The black line in F represent the average CS modulation
351 gain of all tilt- and translation-selective cells, pooled.

352

353 We also analysed CS responses during another illusion-generating motion stimulus, Off-Vertical Axis
354 Rotation (OVAR; **Fig. 7**; see (Laurens et al., 2013b) for details). OVAR consists in tilting the head's
355 vertical axis (**Fig. 7A**, blue) away from vertical and then rotating at a constant speed about that axis.
356 OVAR causes the head to tilt dynamically (**Fig. 7B**), and can be used to demonstrate that Purkinje cells
357 track tilt accurately when the head rotates about its vertical axis (Laurens et al., 2013b). Furthermore,
358 due to the canal's high-pass filter properties, angular velocity signals fade out in ~20 s during OVAR.
359 In this situation, accurate tilt perception is gradually replaced by a translation illusion (Vingerhoets et
360 al., 2006, 2007) (**Fig. 7B**, bottom). In (Laurens et al., 2013b), we demonstrated that the SS firing of tilt-
361 and translation-selective cells match the time course of this motion sensation. Indeed, the modulation
362 of tilt-selective cells decreases (**Fig. 7C**) while the modulation of translation-selective cells increases
363 (**Fig. 7D**) as illusory translation builds up.

364 If indeed CSs occur during real or illusory translation, we expect that both tilt- and translation-selective
365 cells would fire CSs during the late stages, but not the beginning, of OVAR. Further, such a finding
366 would strongly support the hypothesis that CS firing reflects the output of a 3D model of head motion.
367 To test these predictions, we computed the CS modulation gain and phase in both tilt-selective cells
368 (n=14) and translation-selective cells (n=6). We found indeed that CS modulation was low at the
369 beginning of OVAR and increased until it reached a steady-state in both cell types (**Fig. 7, E,F**). When
370 pooled across all cells (**Fig. 7F**, black), the CS response was similar to the SS response of translation-
371 selective cells (**Fig. 7D**).

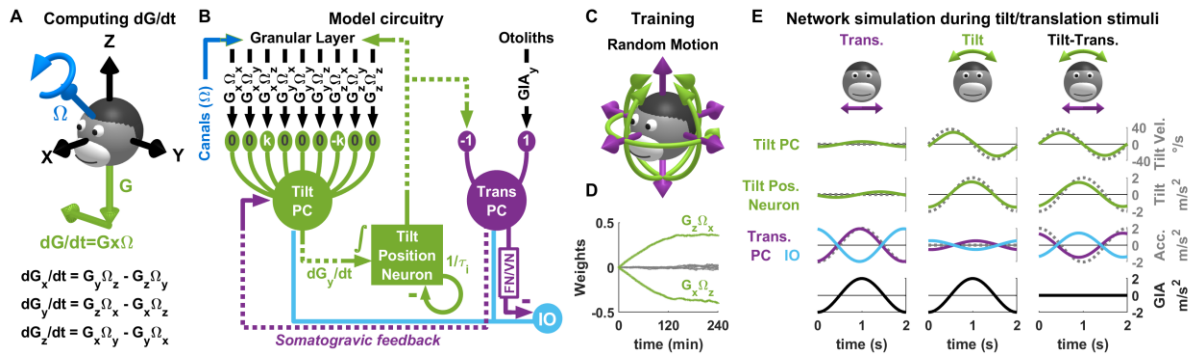
372 Collectively, the results of **Fig. 3-7** demonstrate that CS firing in the NU resembles the SS activity of
373 translation-selective cells during 3D motion and illusory motion. This confirms that CS firing is
374 controlled by neurons that implement 3D internal model computations, as outlined in **Fig. 1D**, and
375 supports the possibility that CS are driven by projections from translation-selective cells onto the IO.
376 Considering that these cells encode a feedback signal when sensory prediction errors occur, and that
377 CS firing is involved in cerebellar learning (Ito, 2006; Kimpo et al., 2014; Lisberger, 1988; Nguyen-Vu
378 et al., 2013), the CS recorded in the NU may participate to a learning mechanism triggered by sensory
379 prediction errors.

380 Neuronal network model

381 The finding that both tilt-selective and translation-selective cells receive similar IO inputs support the
382 hypothesis that they may use the same teaching signal to learn two fundamentally different
383 operations. To test whether this hypothesis is computationally feasible, we designed a neural network
384 model (**Fig. 8A,B**) that reflects the computations outlined in **Fig. 1D**, as described below.

385

386



387 **Figure 8: Neuronal network model of tilt/translation disambiguation.** **A:** Mathematical formulation
 388 of the transformation performed by tilt-selective cells. Converting egocentric rotation signals (Ω blue)
 389 into tilt-velocity (dG/dt , green) requires a vectorial cross-product, whose formula is shown at the
 390 bottom of the panel. **B:** Structure of one olivo-cerebellar loop in the simulated neuron network. This
 391 loop receives otolith inputs (top right) encoding the lateral component of the GIA, i.e. GIA_y . During
 392 learning, the PD of all other cells align with this axis. In the full network, we simulate loops receiving
 393 otolith inputs along all cardinal axes. These loops operate independently, with one exception: the
 394 granular layer upstream of tilt PCs receives output from tilt position neurons from all loops, which
 395 provide the gravity signal G along all dimensions. **C:** The network is trained using random rotations
 396 and translations in 3D. **D:** Evolution of the synaptic weights of a tilt PC encoding dG_y/dt . Bands
 397 represent mean \pm sd over 15 simulations. Green: synaptic weights of the components required to
 398 compute dG_y/dt ; grey: synaptic weights of other components. **F:** Simulated response of all neurons in
 399 the network during tilt, translation and tilt-translation.

400 Tilt-selective PCs (**Fig. 8B**, 'Tilt PC') compute tilt velocity, i.e. the derivative of gravity dG/dt .
 401 Mathematically, tilt velocity can be expressed as the vectorial cross-product $G \times \Omega$, which can be
 402 decomposed into combinations of products (**Fig. 8A**): for instance, lateral tilt velocity, dG_y/dt , is
 403 computed as $G_z\Omega_x - G_x\Omega_z$. We propose that granule cells encode all 9 possible products ($G_x\Omega_x$, $G_x\Omega_y$,
 404 etc; **Fig. 8B**), and that tilt-selective PCs learn to combine these products. For instance, to encode
 405 dG_y/dt (with a gain factor k), a tilt-selective cell would associate a weight of k to $G_z\Omega_x$, $-k$ to $G_x\Omega_z$, and
 406 0 to all other products. In this respect, our model follows the Marr-Albus hypothesis, in which granule
 407 cells act as basis functions (Albus, 1971; Marr, 1969). In (Laurens et al., 2013b; Laurens & Angelaki,
 408 2020), we noted that, even though tilt-selective PCs primarily encode tilt velocity, their firing is
 409 partially shifted toward tilt position. To reproduce this property, we modelled these cells as leaky
 410 integrators with a short time constant of 50ms.

411 The output of tilt-selective PCs is integrated temporally to yield an estimate of tilt position (i.e. G) by
412 “tilt position neurons” (whose nature is currently unknown) (**Fig. 8B**). Since it is questionable whether
413 neurons can perform a perfect integration, we model these neurons as leaky integrators with a time
414 constant of 1.2s. Tilt position neurons project to translation-selective PCs, as well as to the granular
415 layer in which they provide the gravity signal required to compute $G \times \Omega$.

416 Translation-selective PCs (**Fig. 8B**) combine the tilt estimate and the raw otolith signals to compute
417 net translation. The polarity of this connection can be deduced as follows: based on **Fig. 5**, we know
418 that a translation cell with a given PD (e.g. leftward acceleration) receives the same IO input as a tilt-
419 selective cell with an equivalent PD (e.g. rightward tilt velocity, see **Fig. 1B**). Therefore, the pathway
420 between tilt-selective and translation-selective PCs should be altogether *inhibitory*. Note, however,
421 that the actual pathway between tilt-selective and translation-selective cells involves an unknown
422 number of synapses. Here we describe it as an entirely excitatory pathway that terminates with a final
423 inhibitory synapse to the translation-selective PC. In practice, the polarity of the individual connections
424 may be changed without loss of generality.

425 Translation-selective cells also project to tilt-selective cells (**Fig. 8B**; see also **Fig. 1D**), as shown in
426 (Laurens et al., 2013b) to implement a well-known mechanism (Graybiel, 1952) called somatogravic
427 feedback (Laurens & Angelaki, 2011, 2017), which prevents the tilt position neurons from
428 accumulating errors as they integrate noisy inputs over time and compensates for the leaky dynamics
429 of the tilt position neurons.

430 Learning rule

431 Next, we assume that IO signals drive synaptic plasticity according to the following rule (Dean et al.,
432 2002, 2010; Dean & Porrill, 2014):

$$433 \quad \delta w(t) = l \cdot \text{input}(t) \cdot \text{cs}(t)$$

434 Where $\text{input}(t)$ and $\text{cs}(t)$ are the synaptic inputs for a given synapse and the IO inputs, respectively,
435 $\delta w(t)$ is the change of synaptic weight, and l a learning factor. This rule implements a mechanism
436 called ‘decorrelation learning’ (Dean et al., 2002, 2010; Dean & Porrill, 2014) through which the circuit
437 outlined in **Fig. 8B** learns to cancel its otolith input (GIA) based on its canal input (Ω), which amounts
438 to computing a tilt signal. Note that, in this model, this mechanism is more elaborate than in previous
439 work (Dean et al., 2002, 2010; Dean & Porrill, 2014) since it involves a non-linear operation (the cross-
440 product $G \times \Omega$) as well as a temporal integration from tilt velocity to position.

441 A priori, synaptic plasticity could occur at all synapses in the network. However, in the simulated
442 network, any change in the synaptic weight between tilt-selective PCs and tilt position neurons, or

443 between tilt position neurons and translation-selective PCs, can be replaced by an overall gain change
444 of the active synapses of tilt-selective PC. Therefore, for simplicity, we only consider plasticity at the
445 level of tilt-selective PCs.

446

447 Simulation

448 In order to create a full 3D model, we simulated 3 parallel loops that process GIA_x , GIA_y and GIA_z . The
449 tilt position neurons in these 3 loops provide the components G_x , G_y , G_z required to compute $G_x\Omega$. We
450 trained the model during simulated 3D motion (**Fig. 8C,D**), and then simulated all cell types during roll
451 tilt and lateral translation (**Fig. 8B**). The synaptic weights of the tilt-selective PC were initialized
452 randomly (following a Gaussian distribution with a standard deviation of 0.2) priori to training. During
453 training, the weights corresponding to $G_z\Omega_x$ and $G_x\Omega_z$ evolved in opposite directions and stabilized to
454 opposite values (**Fig. 8D**, green), while all other weights decreased to 0 (**Fig. 8D**, grey). This indicates
455 that the synapses of the simulated tilt-selective cells implement the cross-product necessary to
456 compute dG_y/dt .

457 The simulated neuronal responses during tilt/translation paradigms reproduced the prominent
458 properties of tilt- and translation-selective PCs. Tilt-selective PCs responded during tilt (**Fig. 8E**, middle)
459 with a gain of 0.78 relative to tilt velocity and were primarily in phase with tilt velocity, but shifted by
460 11° towards tilt position. During translation (**Fig. 8E**, left), their response gain was largely reduced (4.6
461 times less than during tilt). Tilt position neurons also responded during tilt specifically, with a gain of
462 0.76 and a slight phase lead of 5° relative to tilt position (**Fig. 8E**, middle). Their response to translation
463 (**Fig. 8E**, left) was also much lower (by a factor of 4.8 compared to tilt). In contrast, translation-selective
464 cells responded during translation (**Fig. 8E**, left) with a gain of 0.97 and phase lead of 9° , and their
465 response during tilt was reduced by a factor of 3.8 (**Fig. 8E**, middle). The simulated IO response was
466 the inverse of that of translation-selective PCs. As expected, all cells responded during tilt-translation,
467 and maintained their phase relative to tilt velocity and position (tilt PC and tilt position neurons) or
468 translation (translation PC and IO neurons).

469 Thus, a simple CS-driven learning rule, based on the principle of decorrelation learning, where only
470 translation-selective cells project to the IO, is sufficient to train a neuronal network to integrate
471 rotation signals in 3D so as to predict and cancel tilt-driven activation of the otoliths. These
472 computational models support the experimental finding that a single olivocerebellar loop with a
473 shared error signal underlies the diverse vestibular modulation encountered in the vermal
474 vestibulocerebellum.

475

Discussion

476 Olivo-cerebellar loops form a unit of cerebellar computation (Apps et al., 2018; Apps & Garwicz, 2005;
477 Chaumont et al., 2013; De Zeeuw et al., 2011; Ekerot et al., 1991; Garwicz et al., 1998; Herzfeld et al.,
478 2015; Ozden et al., 2009; Shadmehr, 2020; Sugihara & Qu, 2007). Here we show that two functionally
479 distinct types of PC may implement two computational steps within a single olivo-cerebellar loop.

480 In previous studies (Angelaki et al., 2004; Laurens et al., 2013b; Laurens & Angelaki, 2020; Yakusheva
481 et al., 2007, 2008, 2010), we have identified two distinct groups of PCs defined by their SS properties:
482 Tilt-selective cells encode allocentric velocity relative to gravity which, when integrated, can predict
483 the gravitational force acting on the inner ear's inertial sensors - the otoliths. Translation-selective
484 cells encode otolith prediction error. Yet, the CS properties of both cell types are identical and
485 proportional to the SS firing of translation-selective cells, i.e. to the otolith prediction error. This
486 finding suggests that translation-selective PCs may control the activity of IO cells that innervate them
487 (Chaumont et al., 2013) through their downstream projections to the fastigial or vestibular nuclei.
488 Thus, the output of translation-selective PCs may serve as a dual function - driving behavioural
489 responses and generating a teaching signal to maintain optimal control through the IO loop.

490 The similarity in CS response properties suggests that both types of PCs belong to a single olivo-
491 cerebellar loop. Thus, tilt- and translation-selective cells may form a computational unit that uses its
492 own output as a teaching signal. In this respect, they may implement the decorrelation learning rule
493 proposed by (Dean et al., 2002, 2010; Dean & Porrill, 2014) to explain how efference copies are used
494 to filter out self-generated actions from a sensory signal. The computations performed by tilt- and
495 translation-selective cells are, however, more intricate than the reafference suppression function
496 because they involve a 3D non-linear spatial transformation combined with temporal integration.
497 Indeed, our model simulations confirm that such computations can be learned using a decorrelation
498 learning rule.

499

500 *Tilt- and translation-selective cells form a computational unit*

501 Previous studies (Angelaki et al., 2004; Laurens et al., 2013b; Laurens & Angelaki, 2020) have shown
502 that tilt- and translation-selective cells encode the two interconnected computational steps outlined
503 in **Fig. 1C**. Yet, their functional link had remained tentative without any established neural pathway
504 between tilt-selective and translation-selective PCs. Alternatively, it could be that these properties
505 arise independently in these PC types, perhaps through computations that occur elsewhere, e.g., in

506 the granular layer or the vestibular nuclei. The current finding that both cell types receive identical IO
507 inputs supports the notion that they are functionally linked within the same olivo-cerebellar network.

508 Our findings also provide answers to the following question: if a neuronal pathway links tilt-selective
509 and translation-selective PCs, then, considering that this pathway is likely polysynaptic, is it overall
510 excitatory or inhibitory? For instance, a tilt-selective cell whose SS firing encodes leftward tilt (after
511 temporal integration) may either inhibit a translation-selective cell that encodes rightward
512 acceleration (**Fig. 1B-D**) or activate a translation-selective cell that encodes leftward acceleration. Our
513 finding that cells that prefer e.g. leftward tilt and rightward acceleration would receive identical IO
514 inputs (**Fig. 5**) supports the former possibility, and suggests that the postulated anatomical link is
515 overall inhibitory.

516

517 *Internal model computations for self-motion perception and feedback signals*

518 The concept of internal model is a classical approach for apprehending how the brain processes
519 multisensory self-motion information, proposed as early as the late 70s (Oman, 1982; Ormsby &
520 Young, 1977). Several quantitative models were subsequently developed in the following decades
521 (Borah et al., 1988; Bos & Bles, 2002; Glasauer & Merfeld, 1997; Karmali & Merfeld, 2012; Laurens &
522 Angelaki, 2011, 2017; Laurens & Droulez, 2007; Merfeld, 1995; Zupan et al., 2002), whose findings
523 have been extensively validated by behavioural (Angelaki et al., 1999; Dakin et al., 2020; Khosravi-
524 Hashemi et al., 2019; Laurens et al., 2010, 2011; Merfeld, 1995; Merfeld et al., 1999) and
525 neurophysiological studies (Angelaki et al., 2004; Cullen, 2012; Cullen & Brooks, 2015; Cullen & Roy,
526 2004; Hernández et al., 2020; Laurens et al., 2013a, 2013a; Laurens & Angelaki, 2020; Shaikh et al.,
527 2005; Stay et al., 2019; Yakusheva et al., 2007, 2008, 2013).

528 Whereas early studies have focused on passive motion (Angelaki et al., 2004; Laurens et al., 2013a,
529 2013a; Laurens & Angelaki, 2020; Shaikh et al., 2005; Yakusheva et al., 2007, 2008, 2013), we have
530 proposed a more general framework (Laurens & Angelaki, 2017) in which cerebellar PCs implement a
531 forward model of the otolith organs, and in which translation-selective cells encode the resulting
532 sensory prediction error.

533 This theoretical hypothesis has already been supported by multiple experimental findings. First,
534 translation-selective cells respond to passive translation. Second, their firing is reduced when other
535 sources of information can be used to predict otolith activity; e.g., efference copy signals during active
536 translations; indeed, the firing of vestibular and fastigial nuclei translation-selective cells is markedly
537 reduced (Carriot et al., 2013; Mackrous et al., 2019) - a finding which presumably generalises to

538 translation-selective PCs in the NU. Further, responses of translation-selective cells is also diminished
539 during tilt, during which rotation signals can be used to track head tilt relative to gravity and predict
540 the gravitational activation of the otoliths (Glasauer & Merfeld, 1997; Laurens & Angelaki, 2017;
541 Merfeld, 1995). Finally, this framework implies that an otolith prediction error, and a corresponding
542 activation of translation-selective cells, should occur whenever rotation signals do not match head
543 motion relative to vertical. We have verified this hypothesis in (Laurens et al., 2013a, 2013b), and
544 shown that the firing of translation-selective neurons reflect these illusory signals (Laurens & Angelaki,
545 2011).

546

547 Neuronal and behavioural outputs of the NU

548 Translation-selective cells have been identified in multiple brain areas: the fastigial and vestibular
549 nuclei (Angelaki et al., 2004; Hernández et al., 2020; Laurens et al., 2013a, 2013a; Laurens & Angelaki,
550 2020; Shaikh et al., 2005; Stay et al., 2019; Yakusheva et al., 2007, 2008, 2013) and the vestibular
551 thalamus (Dale & Cullen, 2017).

552 In contrast, tilt-selective cells have, to date, only been formally identified in the NU. This may be
553 because identifying cells that encode rotation velocity relative to vertical requires distinguishing them
554 from semicircular canal-driven cells that encode rotation velocity in egocentric coordinates. Tilt-
555 selective cells and canal-driven cells have similar responses during simple rotations about earth-
556 vertical or earth-horizontal axes, as in e.g. **Fig. 2,5**. Therefore, formally identifying tilt-selective cells
557 requires testing their responses during multiple 3D rotation protocols, e.g., as in **Fig. 7**, which has only
558 been done in the NU so far (Laurens et al., 2013b). For example, some rotation-selective neurons in
559 the vestibular and fastigial nuclei (Buettner et al., 1978; Büttner et al., 2003; Siebold et al., 1997;
560 Waespe & Henn, 1979) have been presented as tilt-selective (Mackrous et al., 2019), but it is currently
561 unknown whether these cells encode tilt, as opposed to egocentric rotation. Note that tilt signals have
562 been identified in the navigation system (Angelaki et al., 2020), but these cells were not tested during
563 tilt/translation discrimination protocols, thus it is unknown whether they convey a net tilt signal.
564 Although tilt perception is driven by a 3D internal model in humans (Clark & Graybiel, 1966; Merfeld
565 et al., 2001; Niehof et al., 2019a, 2019b; Vingerhoets et al., 2007), whether tilt-selective cells exist
566 outside the NU remains unknown.

567 Beyond self-motion perception, the NU innervates regions of the fastigial nucleus that are involved in
568 attention, vigilance and hippocampal function (Fujita et al., 2020), suggesting a possible consequence
569 of otolith prediction errors for a variety of brain functions.

570

571 *Anatomical substrate of the olivo-cerebellar loop with the NU*

572 Olivo-cerebellar loops in the NU have been studied in rabbits (Barmack & Shojaku, 1995; Fushiki &
573 Barmack, 1997), mice (Yakhnitsa & Barmack, 2006) and cats (Kitama et al., 2014) using exclusively
574 rotation (but not translation) stimuli. Although it is impossible to test the current hypotheses in the
575 absence of translation stimuli, findings from these studies are consistent with the present results.
576 First, these studies reported SS and CS modulation during tilt, but not during rotations in an earth-
577 horizontal plane. Note that even translation-selective cells show a substantial modulation during tilt
578 (**Fig. 3A, Fig. 5**). It is thus possible that neurons recorded in previous studies reflected a mixture of tilt-
579 selective and translation-selective cells. In fact, one study (Kitama et al., 2014) noted that NU cells
580 could respond in phase with either tilt position or velocity. Considering that tilt-selective cells encode
581 velocity (Laurens & Angelaki, 2020), ‘velocity’ cells likely correspond to tilt-selective cells, whereas
582 ‘position’ cells likely correspond to translation-selective cells. This interpretation is corroborated by
583 the SS modulation gain during tilt at 0.5Hz: 133 and 64 spk/s/G respectively for ‘velocity’ and ‘position’
584 cells respectively in (Kitama et al., 2014), that match our recordings (**Fig. 3A**). Furthermore, previous
585 studies also found that CSs occur in antiphase with SSs, in agreement with our observations (**Fig. 5**).
586 Altogether, these similarities indicate that the NU PCs reported to be modulated by tilt in (Barmack &
587 Shojaku, 1995; Fushiki & Barmack, 1997; Kitama et al., 2014; Yakhnitsa & Barmack, 2006) likely
588 correspond to both tilt- and translation-selective cells.

589 The medial portion of the NU receives projections from two regions of the IO. The first, which is
590 composed of the dorsal cap and ventrolateral outgrowth, carries visual optokinetic signals (Barmack
591 & Hess, 1980; Leonard et al., 1988) to a small medial portion of the nodulus. Since our experiments
592 were performed in darkness, this region is unlikely to account for the CS responses studied here. The
593 second IO region is the beta nucleus (Barmack, Fagerson, Fredette, et al., 1993; Voogd et al., 1996),
594 which receives projections from the medial and descending vestibular nuclei (Balaban & Beryozkin,
595 1994; Barmack, Fagerson, & Errico, 1993; Gerrits et al., 1985; Saint-Cyr & Courville, 1979; Turecek &
596 Regehr, 2020) and the parasolitary nucleus (Barmack, 2006; Barmack & Yakhnitsa, 2000). In turn, the
597 medial and descending vestibular nuclei receive projection from the NU (Bernard, 1987; Epema et al.,
598 1985; Shojaku et al., 1987; Wylie et al., 1994), as well as the parasolitary nucleus (Barmack,
599 unpublished observations reported in (Barmack & Yakhnitsa, 2000), and R. Sillitoe, personal
600 communication). Thus, the anatomical substrate of the olivo-cerebellar loop involving tilt and
601 translation-selective cells may include a projection of the NU to the beta nucleus through the medial
602 and descending vestibular and parasolitary nuclei. In agreement with this hypothesis, translation-

603 selective cells exist in the vestibular nuclei (Angelaki et al., 2004; Zhou et al., 2006); the firing of
604 neurons in the parasolitary and beta nuclei is similar to the CS responses in the NU (Barmack, Fagerson,
605 Fredette, et al., 1993; Barmack & Yakhnitsa, 2000), and Fos expression studies indicate that the beta
606 nucleus is activated by linear accelerations (Li et al., 2013).

607

608 Conclusion

609 From an experimenter's point of view, linking neural circuits and theoretical predictions may appear
610 an arduous if not vain undertaking, since abstract concepts such as internal models and Kalman
611 filtering may seem too far remote from physiological reality, if not plainly "too nice". Indeed, we too
612 are amazed that the vestibulo-cerebellar circuit should consistently reflect such theorized
613 computations. And yet, these findings should not come as a surprise, since behavioural studies have
614 consistently shown that the brain implements the building blocks of internal models, which are nicely
615 mathematically tractable in a well-defined computational challenge such as tilt/translation
616 discrimination. Thus, when theoretical concepts have passed the test of decades of scrutiny, we
617 should expect to find their embodiment in neuronal circuits.

618

619 **Acknowledgements**

620 The work was supported by NIH grant DC004260.

621 **Methods**

622 Animals

623 Three male rhesus Macaques, aged 3, 4 and 9 years, were used in the study. The animals were pair-
624 housed in a vivarium under normal day/night cycle illumination. Experimental procedures were in
625 accordance with US National Institutes of Health guidelines and approved by the Animal Studies
626 Committee at Washington University in St Louis (approval n°20100230).

627 Experimental procedures and neuronal recordings

628 Experimental procedures were described in detail in (Laurens et al., 2013a, 2013b). In summary,
629 animals were seated in primate chairs that were installed on a 3-axes rotator mounted on a linear sled
630 (Acutronics Inc, Pittsburg, PA). We recorded neurons extracellularly using epoxy-coated tungsten
631 electrodes (5 or 20 M Ω impedance; FHC, Bowdoinham, ME). Recording locations were determined
632 stereotaxically and relative to the abducens nucleus. Raw spiking data was sorted offline using custom
633 Matlab scripts, based on spike amplitude and principal components analysis. In this study, we included
634 only neurons where CS firing could be isolated consistently across trials, and where CS were followed
635 by a pause in SS firing for at least 10 ms.

636 Experimental protocols

637 Sinusoidal tilt and translation stimuli (**Fig. 2A**) consisted of translation (peak acceleration = 0.2 g, with
638 $g = 9.81 \text{ m/s}^2$) or tilt (peak tilt = 11.5°) oscillations at 0.5 Hz, or combinations of these stimuli (out of
639 phase: tilt-translation or in phase: tilt+translation). Stimuli could be delivered along the head's naso-
640 occipital axis (forward/backward translation and pitch tilt), lateral axis (left/right translation and roll
641 tilt) or along intermediate axes. We recorded the responses of each cell using stimuli along at least
642 two head axes.

643 Tilt while rotating (TWR) (Laurens et al., 2013a) consists of rotating the setup about a fixed earth-
644 vertical axis at a constant velocity of 45°/s. During this rotation, animals were tilted back and forth
645 $\pm 10^\circ$ along one plane (i.e. pitch, roll or intermediate) about the vertical axis. Tilt movements were brief
646 movements (peak velocity 20°/s, acceleration 50°/s², duration 1.4s) that were separated by 30s of
647 fixed tilt.

648 Off-vertical axis rotation (OVAR) (Laurens et al., 2013b) consisted in tilting the animal by 10°, and then
649 rotating around the head's vertical axis at 180°/s (peak acceleration: 90°/s²) for 80s. This resulted in
650 the head tilting in a sequence (nose up, left ear down, nose down, right ear down, nose up) which is
651 physically equivalent to out-of-phase oscillations in pitch and roll, with 10° peak tilt, at 0.5 Hz.

652 Data analysis

653 SS and CS firing were analysed using the same methods as in (Laurens et al., 2013a, 2013b). We also
654 refer the reader to (Laurens & Angelaki, 2016) for an in-depth presentation of the analysis of sinusoidal
655 tilt and translation stimuli. In this section, we present some analyses that were specifically developed
656 or modified in the present study.

657 *Modulation amplitude:* The only difference between the analysis of SS and CS was the way modulation
658 amplitude was computed. To quantify the modulation of SS, we fitted firing histograms with a rectified
659 sinusoid function: $FR(t) = \max(0; FR_0 + A \cdot \cos(\pi \cdot \omega \cdot t + \phi))$ where ω is the stimulus frequency in Hz, A and
660 ϕ the response amplitude and phase and FR_0 the cell's baseline firing. To quantify the modulation of
661 CS, we performed a simple Fourier transform, which is equivalent to fitting firing histograms with a
662 sinusoid $FR(t) = FR_0 + A \cdot \cos(\pi \cdot \omega \cdot t + \phi)$, without rectification. We chose this approach because using a
663 rectified function yields more accurate results for cells where the firing becomes 'less than 0' in the
664 trough of the firing histograms, but is unreliable when cells discharge a low number of spikes, which
665 is the case with CS.

666 *Response PD and phase:* In **Fig. 4**, we summarize the cells' firing properties by computing the PD and
667 response phase of SS and CS. For instance, a cell may respond to leftward acceleration with a phase
668 lead of 10° . However, it is equivalent to this cell responding to rightward acceleration with a phase
669 lead of -170° . In order to express the PD and phase of SS and CS in a coherent manner, we adopt the
670 following procedures. First, we compute the PD and phase of SS. For translation-selective cells, we
671 express the PD such that the response phase during translation is within $\pm 90^\circ$ (in the example above,
672 the PD would be to the left). For tilt-selective cells, we express it such that the response phase during
673 tilt is always within $54 \pm 90^\circ$: this is because tilt-selective cells encode a mixture of tilt velocity and
674 position, with a mean response phase of 54° at the population level (Laurens et al., 2013b), and
675 therefore it is logical to express response phase in an interval centred around that value. For other cell
676 types, we proceed as for translation-selective cells. Note that this convention has no impact on our
677 statistical analyses but only serves to make figures clearer (e.g. in **Fig. 4C**).

678 Next, we compute the PD and phase of CS, independently from the SS response. In a second step, if
679 the PDs of SS and CS are more than 90° apart, we invert both the PD and phase of CS. In absolute
680 terms, these conventions do not change how we measure the SS and CS responses, since reversing
681 both the PD and phase results in an equivalent description of the response. Note that, using these
682 conventions, (1) the absolute difference between the PD of SS and CS is always less than 90° (**Fig.**
683 **4A,B**); (2) the phase of SS is expressed as a circular variable with a periodicity of 180° ; whereas (3) the
684 phase of CS is a circular variable with a periodicity of 360° (**Fig. 4C,D**).

685 *Regression analysis:* We tested whether CS firing can be related to the SS output of PC populations by
686 performing a multiple regression analysis, where the dependent variable was the average CS firing in
687 the NU (CS_{NU}) and the predictors were the SS firing of translation-, tilt- and GIA-selective cells (SS_{trans} ,
688 SS_{tilt} and SS_{GIA}). We constructed a vector SS_{trans} that contains the SS firing histograms of translation-
689 selective cells during translation, tilt and tilt-translation (i.e. the three black histograms in Fig. 5A,
690 concatenated one after another). We constructed the vectors SS_{tilt} and SS_{GIA} similarly. Finally, we
691 constructed a similar vector CS_{NU} by averaging the CS firing of all translation-, tilt- and GIA-selective
692 cells. Next, we build a quadratic regression model:

$$693 \quad CS_{NU} = a + b.SS_{trans} + c.SS_{trans}^2 + d.SS_{tilt} + e.SS_{tilt}^2 + f.SS_{GIA} + g.SS_{GIA}^2$$

694

695 We evaluated the goodness of fit of the regression by computing the squared coefficient of correlation
696 $R^2 = 1 - SSR/SS_{tot}$ where SSR is the sum of squared residuals and SS_{tot} the variance of CS_{NU} . To measure
697 the contribution of each SS response type, we computed partial R^2 , e.g. for translation-selective cells,
698 we computed $pR^2_{trans} = 1 - SSR/SSR_{trans}$, where SSR_{trans} is the sum of squared residuals obtained when
699 translation-selective cells are excluded from the regression. A large/small pR^2 indicates that including
700 a given response type has a large/small impact on the regression's goodness of fit, implying that SS
701 from the corresponding population of PC contribute to a large/small extent to controlling CS firing.
702 We used a shuffling approach to estimate the confidence intervals of pR^2 : we computed 10000
703 shuffled values of pR^2_{trans} , for each of which the vector SS_{trans} was shuffled, and defined the confidence
704 interval (at $\alpha = 1\%$) as the 99-percentile of the distribution of shuffled values. We performed the same
705 computation for pR^2_{tilt} and pR^2_{GIA} . We found that the 99-percentile is equal to 0.16 in all cases, i.e. pR^2
706 values lower than 0.16 were not significantly different from 0.

707

708 References

- 709 Albus, J. S. (1971). A theory of cerebellar function. *Mathematical Biosciences*, *10*(1–2), 25–61.
710 [https://doi.org/10.1016/0025-5564\(71\)90051-4](https://doi.org/10.1016/0025-5564(71)90051-4)
- 711 Angelaki, D. E., McHenry, M. Q., Dickman, J. D., Newlands, S. D., & Hess, B. J. M. (1999). Computation
712 of Inertial Motion: Neural Strategies to Resolve Ambiguous Otolith Information. *The Journal*
713 *of Neuroscience*, *19*(1), 316–327. <https://doi.org/10.1523/JNEUROSCI.19-01-00316.1999>
- 714 Angelaki, D. E., Ng, J., Abrego, A. M., Cham, H. X., Asproдини, E. K., Dickman, J. D., & Laurens, J. (2020).
715 A gravity-based three-dimensional compass in the mouse brain. *Nature Communications*,
716 *11*(1), 1855. <https://doi.org/10.1038/s41467-020-15566-5>
- 717 Angelaki, D. E., Shaikh, A. G., Green, A. M., & Dickman, J. D. (2004). Neurons compute internal models
718 of the physical laws of motion. *Nature*, *430*(6999), 560–564.
719 <https://doi.org/10.1038/nature02754>
- 720 Apps, R., & Garwicz, M. (2005). Anatomical and physiological foundations of cerebellar information
721 processing. *Nature Reviews Neuroscience*, *6*(4), 297–311. <https://doi.org/10.1038/nrn1646>
- 722 Apps, R., Hawkes, R., Aoki, S., Bengtsson, F., Brown, A. M., Chen, G., Ebner, T. J., Isope, P., Jörntell, H.,
723 Lackey, E. P., Lawrenson, C., Lumb, B., Schonewille, M., Sillitoe, R. V., Spaeth, L., Sugihara, I.,
724 Valera, A., Voogd, J., Wylie, D. R., & Ruigrok, T. J. H. (2018). Cerebellar Modules and Their Role
725 as Operational Cerebellar Processing Units. *The Cerebellum*, *17*(5), 654–682.
726 <https://doi.org/10.1007/s12311-018-0952-3>
- 727 Balaban, C. D., & Beryozkin, G. (1994). Organization of vestibular nucleus projections to the caudal
728 dorsal cap of kooy in rabbits. *Neuroscience*, *62*(4), 1217–1236. [https://doi.org/10.1016/0306-](https://doi.org/10.1016/0306-4522(94)90354-9)
729 [4522\(94\)90354-9](https://doi.org/10.1016/0306-4522(94)90354-9)
- 730 Barmack, N. H. (2006). Inferior olive and oculomotor system. In *Progress in Brain Research* (Vol. 151,
731 pp. 269–291). Elsevier. [https://doi.org/10.1016/S0079-6123\(05\)51009-4](https://doi.org/10.1016/S0079-6123(05)51009-4)
- 732 Barmack, N. H., Fagerson, M., & Errico, P. (1993). Cholinergic projection to the dorsal cap of the inferior
733 olive of the rat, rabbit, and monkey. *The Journal of Comparative Neurology*, *328*(2), 263–281.
734 <https://doi.org/10.1002/cne.903280208>
- 735 Barmack, N. H., Fagerson, M., Fredette, B. J., Mugnaini, E., & Shojaku, H. (1993). Activity of neurons in
736 the beta nucleus of the inferior olive of the rabbit evoked by natural vestibular stimulation.
737 *Experimental Brain Research*, *94*(2). <https://doi.org/10.1007/BF00230288>
- 738 Barmack, N. H., & Hess, D. T. (1980). Multiple-unit activity evoked in dorsal cap of inferior olive of the
739 rabbit by visual stimulation. *Journal of Neurophysiology*, *43*(1), 151–164.
740 <https://doi.org/10.1152/jn.1980.43.1.151>
- 741 Barmack, N. H., & Shojaku, H. (1995). Vestibular and visual climbing fiber signals evoked in the uvula-
742 nodulus of the rabbit cerebellum by natural stimulation. *Journal of Neurophysiology*, *74*(6),
743 2573–2589. <https://doi.org/10.1152/jn.1995.74.6.2573>
- 744 Barmack, N. H., & Yakhnitsa, V. (2000). Vestibular Signals in the Parasolitary Nucleus. *Journal of*
745 *Neurophysiology*, *83*(6), 3559–3569. <https://doi.org/10.1152/jn.2000.83.6.3559>
- 746 Bernard, J.-F. (1987). Topographical organization of olivocerebellar and corticonuclear connections in
747 the rat? An WGA-HRP study: I. Lobules IX, X, and the flocculus. *The Journal of Comparative*
748 *Neurology*, *263*(2), 241–258. <https://doi.org/10.1002/cne.902630207>
- 749 Borah, J., Young, L. R., & Curry, R. E. (1988). Optimal Estimator Model for Human Spatial Orientation
750 ^a. *Annals of the New York Academy of Sciences*, *545*(1), 51–73. [https://doi.org/10.1111/j.1749-](https://doi.org/10.1111/j.1749-6632.1988.tb19555.x)
751 [6632.1988.tb19555.x](https://doi.org/10.1111/j.1749-6632.1988.tb19555.x)
- 752 Bos, J. E., & Bles, W. (2002). Theoretical considerations on canal-otolith interaction and an observer
753 model. *Biological Cybernetics*, *86*(3), 191–207. <https://doi.org/10.1007/s00422-001-0289-7>
- 754 Buettner, U. W., Buttner, U., & Henn, V. (1978). Transfer characteristics of neurons in vestibular nuclei
755 of the alert monkey. *Journal of Neurophysiology*, *41*(6), 1614–1628.
756 <https://doi.org/10.1152/jn.1978.41.6.1614>
- 757 Büttner, U., Glasauer, S., Glonti, L., Guan, Y., Kipiani, E., Kleine, J., Siebold, C., Tchelidze, T., & Wilden,
758 A. (2003). Multimodal Signal Integration in Vestibular Neurons of the Primate Fastigial

- 759 Nucleus. *Annals of the New York Academy of Sciences*, 1004(1), 241–251.
760 <https://doi.org/10.1196/annals.1303.021>
- 761 Carriot, J., Brooks, J. X., & Cullen, K. E. (2013). Multimodal Integration of Self-Motion Cues in the
762 Vestibular System: Active versus Passive Translations. *Journal of Neuroscience*, 33(50), 19555–
763 19566. <https://doi.org/10.1523/JNEUROSCI.3051-13.2013>
- 764 Cerminara, N. L., Garwicz, M., Darch, H., Houghton, C., Marple-Horvat, D. E., & Apps, R. (2020). *Action-*
765 *based organization and function of cerebellar cortical microcircuits* [Preprint]. Neuroscience.
766 <https://doi.org/10.1101/2020.04.04.025387>
- 767 Chaumont, J., Guyon, N., Valera, A. M., Dugue, G. P., Popa, D., Marcaggi, P., Gautheron, V., Reibel-
768 Foisset, S., Dieudonne, S., Stephan, A., Barrot, M., Cassel, J.-C., Dupont, J.-L., Doussau, F.,
769 Poulain, B., Selimi, F., Lena, C., & Isope, P. (2013). Clusters of cerebellar Purkinje cells control
770 their afferent climbing fiber discharge. *Proceedings of the National Academy of Sciences*,
771 110(40), 16223–16228. <https://doi.org/10.1073/pnas.1302310110>
- 772 Clark, B., & Graybiel, A. (1966). Factors Contributing to the Delay in the Perception of the Oculogravic
773 Illusion. *The American Journal of Psychology*, 79(3), 377. <https://doi.org/10.2307/1420878>
- 774 Cullen, K. E. (2012). The vestibular system: Multimodal integration and encoding of self-motion for
775 motor control. *Trends in Neurosciences*, 35(3), 185–196.
776 <https://doi.org/10.1016/j.tins.2011.12.001>
- 777 Cullen, K. E., & Brooks, J. X. (2015). Neural Correlates of Sensory Prediction Errors in Monkeys:
778 Evidence for Internal Models of Voluntary Self-Motion in the Cerebellum. *The Cerebellum*,
779 14(1), 31–34. <https://doi.org/10.1007/s12311-014-0608-x>
- 780 Cullen, K. E., & Roy, J. E. (2004). Signal Processing in the Vestibular System During Active Versus Passive
781 Head Movements. *Journal of Neurophysiology*, 91(5), 1919–1933.
782 <https://doi.org/10.1152/jn.00988.2003>
- 783 Dakin, C. J., Kumar, P., Forbes, P. A., Peters, A., & Day, B. L. (2020). Variance based weighting of
784 multisensory head rotation signals for verticality perception. *PLOS ONE*, 15(1), e0227040.
785 <https://doi.org/10.1371/journal.pone.0227040>
- 786 Dale, A., & Cullen, K. E. (2017). The Ventral Posterior Lateral Thalamus Preferentially Encodes
787 Externally Applied Versus Active Movement: Implications for Self-Motion Perception. *Cerebral*
788 *Cortex*, 29(1), 305–318. <https://doi.org/10.1093/cercor/bhx325>
- 789 De Zeeuw, C. I., Hoebeek, F. E., Bosman, L. W. J., Schonewille, M., Witter, L., & Koekkoek, S. K. (2011).
790 Spatiotemporal firing patterns in the cerebellum. *Nature Reviews Neuroscience*, 12(6), 327–
791 344. <https://doi.org/10.1038/nrn3011>
- 792 Dean, P., & Porrill, J. (2014). Decorrelation Learning in the Cerebellum. In *Progress in Brain Research*
793 (Vol. 210, pp. 157–192). Elsevier. <https://doi.org/10.1016/B978-0-444-63356-9.00007-8>
- 794 Dean, P., Porrill, J., Ekerot, C.-F., & Jörntell, H. (2010). The cerebellar microcircuit as an adaptive filter:
795 Experimental and computational evidence. *Nature Reviews Neuroscience*, 11(1), 30–43.
796 <https://doi.org/10.1038/nrn2756>
- 797 Dean, P., Porrill, J., & Stone, J. V. (2002). Decorrelation control by the cerebellum achieves oculomotor
798 plant compensation in simulated vestibulo-ocular reflex. *Proceedings of the Royal Society of*
799 *London. Series B: Biological Sciences*, 269(1503), 1895–1904.
800 <https://doi.org/10.1098/rspb.2002.2103>
- 801 Einstein, A. (1907). Über das Relativitätsprinzip und die aus demselben gezogenen Folgerungen, Jahrb.
802 D. Radioaktivität u. Elektronik. IV, 454.
- 803 Ekerot, C. F., Garwicz, M., & Schouenborg, J. (1991). Topography and nociceptive receptive fields of
804 climbing fibres projecting to the cerebellar anterior lobe in the cat. *The Journal of Physiology*,
805 441(1), 257–274. <https://doi.org/10.1113/jphysiol.1991.sp018750>
- 806 Epema, A. H., Guldmond, J. M., & Voogd, J. (1985). Reciprocal connections between the caudal vermis
807 and the vestibular nuclei in the rabbit. *Neuroscience Letters*, 57(3), 273–278.
808 [https://doi.org/10.1016/0304-3940\(85\)90504-X](https://doi.org/10.1016/0304-3940(85)90504-X)

- 809 Fujita, H., Kodama, T., & du Lac, S. (2020). Modular output circuits of the fastigial nucleus for diverse
810 motor and nonmotor functions of the cerebellar vermis. *ELife*, 9, e58613.
811 <https://doi.org/10.7554/eLife.58613>
- 812 Fushiki, H., & Barmack, N. H. (1997). Topography and Reciprocal Activity of Cerebellar Purkinje Cells in
813 the Uvula-Nodulus Modulated by Vestibular Stimulation. *Journal of Neurophysiology*, 78(6),
814 3083–3094. <https://doi.org/10.1152/jn.1997.78.6.3083>
- 815 Garwicz, M., Ekerot, C.-F., & Jörntell, H. (1998). Organizational Principles of Cerebellar Neuronal
816 Circuitry. *Physiology*, 13(1), 26–32. <https://doi.org/10.1152/physiologyonline.1998.13.1.26>
- 817 Gerrits, N. M., Voogd, J., & Magras, I. N. (1985). Vestibular afferents of the inferior olive and the
818 vestibulo-olivo-cerebellar climbing fiber pathway to the flocculus in the cat. *Brain Research*,
819 332(2), 325–336. [https://doi.org/10.1016/0006-8993\(85\)90601-8](https://doi.org/10.1016/0006-8993(85)90601-8)
- 820 Glasauer, S., & Merfeld, D. M. (1997). Modelling three-dimensional vestibular responses during
821 complex motion stimulation. In *Three-dimensional kinematics of eye, head and limb*
822 *movements* (pp. 387–398).
- 823 Graybiel, A. (1952). Oculogravic illusion. *AMA Archives of Ophthalmology*, 48(5), 605–615.
- 824 Green, A. M., Shaikh, A. G., & Angelaki, D. E. (2005). Sensory vestibular contributions to constructing
825 internal models of self-motion. *Journal of Neural Engineering*, 2(3), S164–S179.
826 <https://doi.org/10.1088/1741-2560/2/3/S02>
- 827 Hernández, R. G., De Zeeuw, C. I., Zhang, R., Yakusheva, T. A., & Blazquez, P. M. (2020). Translation
828 information processing is regulated by protein kinase C-dependent mechanism in Purkinje
829 cells in murine posterior vermis. *Proceedings of the National Academy of Sciences*, 202002177.
830 <https://doi.org/10.1073/pnas.2002177117>
- 831 Herzfeld, D. J., Kojima, Y., Soetedjo, R., & Shadmehr, R. (2015). Encoding of action by the Purkinje cells
832 of the cerebellum. *Nature*, 526(7573), 439–442. <https://doi.org/10.1038/nature15693>
- 833 Herzfeld, D. J., Kojima, Y., Soetedjo, R., & Shadmehr, R. (2018). Encoding of error and learning to
834 correct that error by the Purkinje cells of the cerebellum. *Nature Neuroscience*, 21(5), 736–
835 743. <https://doi.org/10.1038/s41593-018-0136-y>
- 836 Hess, B. J. M., & Angelaki, D. E. (1999). Oculomotor Control of Primary Eye Position Discriminates
837 Between Translation and Tilt. *Journal of Neurophysiology*, 81(1), 394–398.
838 <https://doi.org/10.1152/jn.1999.81.1.394>
- 839 Ito, M. (2006). Cerebellar circuitry as a neuronal machine. *Progress in Neurobiology*, 78(3–5), 272–
840 303. <https://doi.org/10.1016/j.pneurobio.2006.02.006>
- 841 Karmali, F., & Merfeld, D. M. (2012). A distributed, dynamic, parallel computational model: The role
842 of noise in velocity storage. *Journal of Neurophysiology*, 108(2), 390–405.
843 <https://doi.org/10.1152/jn.00883.2011>
- 844 Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in*
845 *Neurobiology*, 9(6), 718–727. [https://doi.org/10.1016/S0959-4388\(99\)00028-8](https://doi.org/10.1016/S0959-4388(99)00028-8)
- 846 Khosravi-Hashemi, N., Forbes, P. A., Dakin, C. J., & Blouin, J. (2019). Virtual signals of head rotation
847 induce gravity-dependent inferences of linear acceleration. *The Journal of Physiology*,
848 597(21), 5231–5246. <https://doi.org/10.1113/JP278642>
- 849 Kimpo, R. R., Rinaldi, J. M., Kim, C. K., Payne, H. L., & Raymond, J. L. (2014). Gating of neural error
850 signals during motor learning. *ELife*, 3, e02076. <https://doi.org/10.7554/eLife.02076>
- 851 Kitama, T., Komagata, J., Ozawa, K., Suzuki, Y., & Sato, Y. (2014). Plane-specific Purkinje cell responses
852 to vertical head rotations in the cat cerebellar nodulus and uvula. *Journal of Neurophysiology*,
853 112(3), 644–659. <https://doi.org/10.1152/jn.00029.2014>
- 854 Kostadinov, D., Beau, M., Pozo, M. B., & Häusser, M. (2019). Predictive and reactive reward signals
855 conveyed by climbing fiber inputs to cerebellar Purkinje cells. *Nature Neuroscience*, 22(6),
856 950–962. <https://doi.org/10.1038/s41593-019-0381-8>
- 857 Laurens, J., & Angelaki, D. E. (2011). The functional significance of velocity storage and its dependence
858 on gravity. *Experimental Brain Research*, 210(3–4), 407–422. [https://doi.org/10.1007/s00221-](https://doi.org/10.1007/s00221-011-2568-4)
859 [011-2568-4](https://doi.org/10.1007/s00221-011-2568-4)

- 860 Laurens, J., & Angelaki, D. E. (2016). How the Vestibulocerebellum Builds an Internal Model of Self-
861 motion. In *The Neuronal Codes of the Cerebellum* (pp. 97–115). Elsevier.
862 <https://doi.org/10.1016/B978-0-12-801386-1.00004-6>
- 863 Laurens, J., & Angelaki, D. E. (2017). A unified internal model theory to resolve the paradox of active
864 versus passive self-motion sensation. *Elife*, *6*, e28074.
- 865 Laurens, J., & Angelaki, D. E. (2020). Simple spike dynamics of Purkinje cells in the macaque vestibulo-
866 cerebellum during passive whole-body self-motion. *Proceedings of the National Academy of*
867 *Sciences*, *117*(6), 3232–3238. <https://doi.org/10.1073/pnas.1915873117>
- 868 Laurens, J., & Droulez, J. (2007). Bayesian processing of vestibular information. *Biological Cybernetics*,
869 *96*(4), 389–404.
- 870 Laurens, J., Meng, H., & Angelaki, D. E. (2013a). Computation of linear acceleration through an internal
871 model in the macaque cerebellum. *Nature Neuroscience*, *16*(11), 1701–1708.
872 <https://doi.org/10.1038/nn.3530>
- 873 Laurens, J., Meng, H., & Angelaki, D. E. (2013b). Neural Representation of Orientation Relative to
874 Gravity in the Macaque Cerebellum. *Neuron*, *80*(6), 1508–1518.
875 <https://doi.org/10.1016/j.neuron.2013.09.029>
- 876 Laurens, J., Strauman, D., & Hess, B. J. (2011). Spinning versus Wobbling: How the Brain Solves a
877 Geometry Problem. *Journal of Neuroscience*, *31*(22), 8093–8101.
878 <https://doi.org/10.1523/JNEUROSCI.5900-10.2011>
- 879 Laurens, J., Straumann, D., & Hess, B. J. M. (2010). Processing of Angular Motion and Gravity
880 Information Through an Internal Model. *Journal of Neurophysiology*, *104*(3), 1370–1381.
881 <https://doi.org/10.1152/jn.00143.2010>
- 882 Leonard, C. S., Simpson, J. I., & Graf, W. (1988). Spatial organization of visual messages of the rabbit's
883 cerebellar flocculus. I. Typology of inferior olive neurons of the dorsal cap of Kooy. *Journal of*
884 *Neurophysiology*, *60*(6), 2073–2090. <https://doi.org/10.1152/jn.1988.60.6.2073>
- 885 Li, C., Han, L., Ma, C.-W., Lai, S.-K., Lai, C.-H., Shum, D. K. Y., & Chan, Y.-S. (2013). Maturation profile of
886 inferior olivary neurons expressing ionotropic glutamate receptors in rats: Role in coding
887 linear accelerations. *Brain Structure and Function*, *218*(4), 833–850.
888 <https://doi.org/10.1007/s00429-012-0432-3>
- 889 Lisberger, S. (1988). The neural basis for learning of simple motor skills. *Science*, *242*(4879), 728–735.
890 <https://doi.org/10.1126/science.3055293>
- 891 Mackrous, I., Carriot, J., Jamali, M., & Cullen, K. E. (2019). Cerebellar Prediction of the Dynamic Sensory
892 Consequences of Gravity. *Current Biology*, *29*(16), 2698–2710.e4.
893 <https://doi.org/10.1016/j.cub.2019.07.006>
- 894 Marr, D. (1969). A theory of cerebellar cortex. *The Journal of Physiology*, *202*(2), 437–470.
895 <https://doi.org/10.1113/jphysiol.1969.sp008820>
- 896 Merfeld, D. M. (1995). Modeling the vestibulo-ocular reflex of the squirrel monkey during eccentric
897 rotation and roll tilt. *Experimental Brain Research*, *106*(1).
898 <https://doi.org/10.1007/BF00241362>
- 899 Merfeld, D. M., Zupan, L. H., & Gifford, C. A. (2001). Neural Processing of Gravito-Inertial Cues in
900 Humans. II. Influence of the Semicircular Canals During Eccentric Rotation. *Journal of*
901 *Neurophysiology*, *85*(4), 1648–1660. <https://doi.org/10.1152/jn.2001.85.4.1648>
- 902 Merfeld, D. M., Zupan, L., & Peterka, R. J. (1999). Humans use internal models to estimate gravity and
903 linear acceleration. *Nature*, *398*(6728), 615–618. <https://doi.org/10.1038/19303>
- 904 Nguyen-Vu, T. B., Kimpo, R. R., Rinaldi, J. M., Kohli, A., Zeng, H., Deisseroth, K., & Raymond, J. L. (2013).
905 Cerebellar Purkinje cell activity drives motor learning. *Nature Neuroscience*, *16*(12), 1734.
- 906 Niehof, N., Perdreau, F., Koppen, M., & Medendorp, W. P. (2019a). Contributions of optostatic and
907 optokinetic cues to the perception of vertical. *Journal of Neurophysiology*, *122*(2), 480–489.
908 <https://doi.org/10.1152/jn.00740.2018>

- 909 Niehof, N., Perdreau, F., Koppen, M., & Medendorp, W. P. (2019b). Time course of the subjective visual
910 vertical during sustained optokinetic and galvanic vestibular stimulation. *Journal of*
911 *Neurophysiology*, 122(2), 788–796. <https://doi.org/10.1152/jn.00083.2019>
- 912 Oman, C. M. (1982). A heuristic mathematical model for the dynamics of sensory conflict and motion
913 sickness. *Acta Oto-Laryngologica*, 94(sup392), 4–44.
- 914 Ormsby, C. C., & Young, L. R. (1977). Integration of semicircular canal and otolith information for
915 multisensory orientation stimuli. *Mathematical Biosciences*, 34(1–2), 1–21.
- 916 Ozden, I., Sullivan, M. R., Lee, H. M., & Wang, S. S.-H. (2009). Reliable Coding Emerges from
917 Coactivation of Climbing Fibers in Microbands of Cerebellar Purkinje Neurons. *Journal of*
918 *Neuroscience*, 29(34), 10463–10473. <https://doi.org/10.1523/JNEUROSCI.0967-09.2009>
- 919 Saint-Cyr, J. A., & Courville, J. (1979). Projection from the vestibular nuclei to the inferior olive in the
920 cat: An autoradiographic and horseradish peroxidase study. *Brain Research*, 165(2), 189–200.
921 [https://doi.org/10.1016/0006-8993\(79\)90553-5](https://doi.org/10.1016/0006-8993(79)90553-5)
- 922 Shadmehr, R. (2020). *Population coding in the cerebellum and its implications for learning from error*
923 [Preprint]. Neuroscience. <https://doi.org/10.1101/2020.05.18.102376>
- 924 Shaikh, A. G., Green, A. M., Ghasia, F. F., Newlands, S. D., Dickman, J. D., & Angelaki, D. E. (2005).
925 Sensory Convergence Solves a Motion Ambiguity Problem. *Current Biology*, 15(18), 1657–
926 1662. <https://doi.org/10.1016/j.cub.2005.08.009>
- 927 Shojaku, H., Sato, Y., Ikarashi, K., & Kawasaki, T. (1987). Topographical distribution of Purkinje cells in
928 the uvula and the nodulus projecting to the vestibular nuclei in cats. *Brain Research*, 416(1),
929 100–112. [https://doi.org/10.1016/0006-8993\(87\)91501-0](https://doi.org/10.1016/0006-8993(87)91501-0)
- 930 Siebold, C., Glonti, L., Glasauer, S., & Büttner, U. (1997). Rostral Fastigial Nucleus Activity in the Alert
931 Monkey During Three-Dimensional Passive Head Movements. *Journal of Neurophysiology*,
932 77(3), 1432–1446. <https://doi.org/10.1152/jn.1997.77.3.1432>
- 933 Stay, T. L., Laurens, J., Sillitoe, R. V., & Angelaki, D. E. (2019). Genetically eliminating Purkinje neuron
934 GABAergic neurotransmission increases their response gain to vestibular motion. *Proceedings*
935 *of the National Academy of Sciences*, 116(8), 3245–3250.
- 936 Sugihara, I., & Quy, P. N. (2007). Identification of aldolase C compartments in the mouse cerebellar
937 cortex by olivocerebellar labeling. *The Journal of Comparative Neurology*, 500(6), 1076–1092.
938 <https://doi.org/10.1002/cne.21219>
- 939 Turecek, J., & Regehr, W. G. (2020). *Synaptic inputs to the inferior olive from cerebellar and vestibular*
940 *nuclei have distinct release kinetics and neurotransmitters* [Preprint]. Neuroscience.
941 <https://doi.org/10.1101/2020.07.31.231290>
- 942 Valera, A. M., Binda, F., Pawlowski, S. A., Dupont, J.-L., Casella, J.-F., Rothstein, J. D., Poulain, B., &
943 Isope, P. (2016). Stereotyped spatial patterns of functional synaptic connectivity in the
944 cerebellar cortex. *eLife*, 5, e09862. <https://doi.org/10.7554/eLife.09862>
- 945 Vingerhoets, R. A. A., Medendorp, W. P., & Van Gisbergen, J. A. M. (2006). Time Course and Magnitude
946 of Illusory Translation Perception During Off-Vertical Axis Rotation. *Journal of*
947 *Neurophysiology*, 95(3), 1571–1587. <https://doi.org/10.1152/jn.00613.2005>
- 948 Vingerhoets, R. A. A., Van Gisbergen, J. A. M., & Medendorp, W. P. (2007). Verticality Perception
949 During Off-Vertical Axis Rotation. *Journal of Neurophysiology*, 97(5), 3256–3268.
950 <https://doi.org/10.1152/jn.01333.2006>
- 951 Voogd, J., Gerrits, N. M., & Ruigrok, T. J. H. (1996). Organization of the Vestibulocerebellum. *Annals of*
952 *the New York Academy of Sciences*, 781(1 Lipids and Sy), 553–579.
953 <https://doi.org/10.1111/j.1749-6632.1996.tb15728.x>
- 954 Waespe, W., & Henn, V. (1979). The velocity response of vestibular nucleus neurons during vestibular,
955 visual, and combined angular acceleration. *Experimental Brain Research*, 37(2).
956 <https://doi.org/10.1007/BF00237718>
- 957 Wolpert, D. M., Miall, R. C., & Kawato, M. (1998a). Internal models in the cerebellum. *Trends in*
958 *Cognitive Sciences*, 2(9), 338–347. [https://doi.org/10.1016/S1364-6613\(98\)01221-2](https://doi.org/10.1016/S1364-6613(98)01221-2)

- 959 Wolpert, D. M., Miall, R. C., & Kawato, M. (1998b). Internal models in the cerebellum. *Trends in*
960 *Cognitive Sciences*, 2(9), 338–347. [https://doi.org/10.1016/S1364-6613\(98\)01221-2](https://doi.org/10.1016/S1364-6613(98)01221-2)
- 961 Wylie, D. R., De Zeeuw, C. I., Digiorgi, P. L., & Simpson, J. I. (1994). Projections of individual purkinje
962 cells of identified zones in the ventral nodulus to the vestibular and cerebellar nuclei in the
963 rabbit. *The Journal of Comparative Neurology*, 349(3), 448–463.
964 <https://doi.org/10.1002/cne.903490309>
- 965 Yakhnitsa, V., & Barmack, N. H. (2006). Antiphase Purkinje cell responses in mouse uvula-nodulus are
966 sensitive to static roll-tilt and topographically organized. *Neuroscience*, 143(2), 615–626.
967 <https://doi.org/10.1016/j.neuroscience.2006.08.006>
- 968 Yakusheva, T. A., Blazquez, P. M., & Angelaki, D. E. (2008). Frequency-Selective Coding of Translation
969 and Tilt in Macaque Cerebellar Nodulus and Uvula. *Journal of Neuroscience*, 28(40), 9997–
970 10009. <https://doi.org/10.1523/JNEUROSCI.2232-08.2008>
- 971 Yakusheva, T. A., Blazquez, P. M., & Angelaki, D. E. (2010). Relationship between Complex and Simple
972 Spike Activity in Macaque Caudal Vermis during Three-Dimensional Vestibular Stimulation.
973 *Journal of Neuroscience*, 30(24), 8111–8126. [https://doi.org/10.1523/JNEUROSCI.5779-
974 09.2010](https://doi.org/10.1523/JNEUROSCI.5779-09.2010)
- 975 Yakusheva, T. A., Blazquez, P. M., Chen, A., & Angelaki, D. E. (2013). Spatiotemporal Properties of Optic
976 Flow and Vestibular Tuning in the Cerebellar Nodulus and Uvula. *Journal of Neuroscience*,
977 33(38), 15145–15160. <https://doi.org/10.1523/JNEUROSCI.2118-13.2013>
- 978 Yakusheva, T. A., Shaikh, A. G., Green, A. M., Blazquez, P. M., Dickman, J. D., & Angelaki, D. E. (2007).
979 Purkinje Cells in Posterior Cerebellar Vermis Encode Motion in an Inertial Reference Frame.
980 *Neuron*, 54(6), 973–985. <https://doi.org/10.1016/j.neuron.2007.06.003>
- 981 Zhou, W., Tang, B. F., Newlands, S. D., & King, W. M. (2006). Responses of Monkey Vestibular-Only
982 Neurons to Translation and Angular Rotation. *Journal of Neurophysiology*, 96(6), 2915–2930.
983 <https://doi.org/10.1152/jn.00013.2006>
- 984 Zupan, L. H., Merfeld, D. M., & Darlot, C. (2002). Using sensory weighting to model the influence of
985 canal, otolith and visual cues on spatial orientation and eye movements. *Biological*
986 *Cybernetics*, 86(3), 209–230. <https://doi.org/10.1007/s00422-001-0290-1>

987