Distinct Representations of Body and Head motion are Dynamically Encoded by Purkinje cell Populations in the Macaque Cerebellum

Short title: Population coding of passive self-motion in the cerebellum

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Abstract

The ability to accurately control our posture and perceive spatial orientation during self-motion requires knowledge of the motion of both the head and body. However, whereas the vestibular sensors and nuclei directly encode head motion, no sensors directly encode body motion. Instead, the integration of vestibular and neck proprioceptive inputs is necessary to transform vestibular information into the body-centric reference frame required for postural control. The anterior vermis of the cerebellum is thought to play a key role in this transformation, yet how its Purkinje cells integrate these inputs or what information they dynamically encode during self-motion remains unknown. Here we recorded the activity of individual anterior vermis Purkinje cells in alert monkeys during passively applied whole-body, body-under-head, and head-on-body rotations. Most neurons dynamically encoded an intermediate representation of self-motion between head and body motion. Notably, these neurons responded to both vestibular and neck proprioceptive stimulation and showed considerable heterogeneity in their response dynamics. Furthermore, their vestibular responses demonstrated tuning in response to changes in head-on-body position. In contrast, a small remaining percentage of neurons sensitive only to vestibular stimulation unambiguously encoded head-in-space motion across conditions. Using a simple population model, we establish that combining responses from ~40-50 Purkinje cells can explain the responses of their target neurons in deep cerebellar nuclei across all self-motion conditions. We propose that the observed heterogeneity in Purkinje cells underlies the cerebellum's capacity to compute the dynamic representation of body motion required to ensure accurate postural control and perceptual stability in our daily lives.
Introduction

The cerebellum guides motor performance by computing differences between the expected versus actual consequences of movements and then adjusting the commands sent to the motor system (reviewed in: Wolpert et al., 1998, Raymond and Medina 2018). Patients with damage to the anterior vermis of the cerebellum show impaired posture and balance, as well as deficits in motor coordination (Dichgans and Diener, 1984; Bastian et al., 1998; Giese et al., 2008; Sullivan et al., 2005; Mitoma et al., 2021). In this context, the anterior vermis has a vital role in the vestibulospinal pathways that generate the postural adjustments required to ensure the maintenance of balance during our everyday activities. Additionally, there is an emerging consensus that the cerebellum contributes to our self-motion perception. Indeed, patients with degeneration of the cerebellar vermis demonstrate reduced perceptual time constants and detection thresholds to externally applied rotations (Bronstein et al. 2008; Dahlem et al., 2016).

The prevailing view is that the vestibular pathways mediating vestibulospinal reflexes and the stable perception of self-motion explicitly transform vestibular information from a head-centered to a body-centered reference frame. The vestibular sensory organs are located within the head, making the vestibular system’s native reference frame head-centered (reviewed in Cullen 2019). In turn, vestibular nerve afferents and their targets in the vestibular nuclei also encode information in a head-centered reference frame (Roy and Cullen 1998, 2001, 2004; Carriot et al. 2013; Brooks and Cullen 2014; Sadeghi et al., 2007; Jamali et al., 2009; Cullen and Minor 2002). However, the brain accounts for the position of the head relative to the body for vestibulospinal reflexes to accurately control the musculature required to maintain upright posture and balance (Tokita et al., 1989, 1991; Kennedy and Inglis 2002). Indeed, distinct representations of body versus head motion are encoded by individual neurons in the fastigial nucleus (Brooks and Cullen 2009, Brooks et al., 2015) - the most medial of deep cerebellar nuclei -which lesion studies have shown serves an important role in the control of posture and balance (Thach et al., 1992; Kurzan et al., 1993; Pelisson et al., 1998). Neck proprioceptors provide the head position information required for this transformation (reviewed in Cullen and Zobeiri 2021). Thus, the integration of neck proprioceptive and vestibular signals is thought to underlie the transformation from a head-centered to a body-centered reference frame in vestibulospinal reflexes pathways as well as our ability to perceive body motion independently of head motion (Mergener et al., 1997; Peterka 2002).

There are many reasons to believe that the anterior region of the cerebellar vermis is vital in the transformation of vestibular information from a head-centered to a body-centered reference frame. First, Purkinje cells in this region project to the rostral portion of the fastigial nucleus (Batton et al., 1977; Yamada and Noda 1987), which lesion studies have shown serves an important role in the control of posture and balance (Thach et al., 1992; Kurzan et al., 1993; Pelisson et al., 1998). Second, inhibition of the cerebellar vermis via continuous theta-burst stimulation impairs the modulation of vestibulospinal pathways that normally accounts for
changes in the position of the head relative to the body (Lam et al., 2016). Third, neuronal recordings from anterior vermis Purkinje cells in decerebrate cats have demonstrated that individual neurons can encode both vestibular and neck proprioceptive-related information (Denoth et al., 1979; Manzoni et al. 1998, 1999, 2004), thereby providing a neural substrate for the coordinate transformation using neck proprioceptive signals to convert head-centered vestibular-signals to a body-centered reference frame. However, these studies stopped short of establishing whether Purkinje cells integrate vestibular and neck proprioceptive signals to dynamically encode head or body movement.

Thus, a key question yet to be answered is: Does the cerebellum integrate vestibular and neck proprioceptive signals to provide a dynamic representation of body motion relative to space? Here we recorded the activity of single Purkinje cells in the anterior vermis during head motion, body motion, and combined head and body motion. We found considerable heterogeneity across individual Purkinje cells in their encoding of head versus body motion, with most (~75%) neurons dynamically encoding an intermediate representation of self-motion between head and body motion. These neurons, termed bimodal neurons, responded to both vestibular and neck proprioceptive stimulation and displayed head-position-dependent tuning in their sensitivity to vestibular stimulation. In contrast, a minority of cells, termed unimodal neurons, only responded to vestibular stimulation and unambiguously encoded the motion of the head in space. Across all cells, the linear combination of a given neuron's response sensitivity to dynamic neck and vestibular stimulation alone well estimated its response during combined stimulation. Finally, we found that a simple linear combination model combining the responses of ~40 Purkinje cells could account for the more homogeneous responses of target neurons in the deep cerebellar nuclei (i.e., the rostral fastigial nucleus) during applied self-motion. Our results provide the first evidence, at the level of single Purkinje cells, that a sequential transformation from a head-centered to body-centered reference frame occurs between the cerebellum and deep cerebellar nucleus to ensure postural and perceptual stability in everyday life.
Results

The most vestibular sensitive Purkinje cells in the anterior vermis are also sensitive to stimulation of neck proprioceptors

Each Purkinje cell in our population (n = 73) was responsive to vestibular stimulation and was insensitive to eye movements. To assess each neuron’s vestibular sensitivity, we applied ipsilaterally and contralaterally directed whole-body rotations in the dark (i.e., whole-body-rotations; see METHODS). As illustrated in Figure 1A, we found considerable heterogeneity in vestibular sensitivities across our Purkinje cell population. Some neurons generated excitatory versus inhibitory responses for oppositely directed head movements (Fig. 1A; left, linear). Alternately, some neurons generated bidirectional excitatory responses (center, v-shaped), while others largely only generated excitatory responses for one movement direction (Fig. 1A; right, rectifying). This contrasts with the vestibular responses recorded in areas targeted by Purkinje cells in the anterior vermis. Notably, vestibular-only neurons in the rFN and vestibular nucleus consistently show excitatory versus inhibitory responses for oppositely directed head movements (rFN: Gardner and Fuchs, 1975, Shaikh et al., 2005; vestibular nucleus: Scudder and Fuchs, 1992, Cullen and McCrea, 1993, McCrea et al., 1999, Roy and Cullen, 2004).

To quantify the vestibular sensitivity of each Purkinje cell in our population, we fit a least-squares dynamic regression model with three kinematic terms (i.e., head-in-space position, velocity, and acceleration) to responses for movements in each direction (Figure 1—supplement 1, see Methods). We found that the preferred movement direction (i.e., the direction that resulted in an excitatory response, or in the greater excitatory response in the case of v-shaped neurons) could be either ipsilateral or contralateral for a given Purkinje cell. Neurons with preferred responses for ipsilaterally (for example, Fig. 1A, right panel (n = 32) or contralaterally (Fig. 1A, left and middle panels n = 41) directed rotations were accordingly classified as Type I or Type II, respectively. Our analysis further revealed that the response dynamics varied considerably across neurons, with 43% neurons demonstrating responses that were relatively in-phase (± 15°) with head velocity (1.8 ± 7.7°), while others demonstrated marked response leads (32%, 57± 31) or lags (25%, -47.5 ± 22°). Figures 1B,C illustrate the vestibular response vectors for our populations of neurons computed in their preferred and non-preferred directions, respectively. The vector represents the gain (length) and phase (angle) of the neural responses to each stimulus computed at 1Hz (see Methods). The large arrows represent average neuronal responses to vestibular stimuli for Type I (S_vest. = 0.42 ± 0.37 (sp/s)/(°/s), Phase_vest. = 6 ± 31°) and Type II neurons (S_vest. = 0.31 ± 0.34 (sp/s)/(°/s), Phase_vest. = 172 ± 42°), respectively.

We next addressed whether the Purkinje cells that responded to vestibular stimulation also responded to the activation of neck proprioceptors. To assess each neuron’s proprioceptive sensitivity, we applied ipsilaterally and contralaterally directed rotations to the monkey’s body
while its head was held stationary relative to space (i.e., body-under-head rotations; see METHODS), with the same motion profiles as those used for the assessment of vestibular sensitivities. Thus, since the head did not move relative to space, neck proprioceptors but not the vestibular system were stimulated in this condition. Figure 2A illustrates the responses recorded from the same three example neurons shown in Figure 1A. We quantified the neck proprioceptive sensitivity of each Purkinje cell using least-squares dynamic regression (see Methods) and found that most neurons ~75% (n = 54) were sensitive to passive proprioceptive stimulation (Fig. 2B&C, filled bars; bimodal neurons), whereas the remaining ~25% (n = 19) were insensitive (Fig. 2 Fig. 2B&C, open bars; unimodal neurons). Overall, similar to our findings above regarding vestibular stimulation, the dynamics of responses to proprioceptive stimulation varied considerably across Purkinje cells (Figure 2—figure supplement 1). The insets in Figures 2B,C illustrate the response vectors for proprioceptive stimulation across our populations of neurons in the preferred and non-preferred directions, respectively. As in Figures 1B,C above, the vector was computed based on the gain (length) and phase (angle) of the neural responses to each stimulus at 1 Hz (see Methods) and large arrows represent average neuronal responses measured in response to proprioceptive stimuli for neurons with Type I ($S_{prop.} = 0.12 \pm 0.44 (sp/s)/(°/s)$, $\text{Phase}_{prop.} = 159 \pm 29°$) versus Type II ($S_{prop.} = 0.13 \pm 0.46 (sp/s)/(°/s)$, $\text{Phase}_{prop.} = -27 \pm 20°$) responses. Furthermore, Purkinje cells showed considerable heterogeneity in their simple spike response dynamics to vestibular versus proprioceptive stimulation (Figure 2—figure supplement 2). Indeed, neurons typically did not show the same patterns (linear, v-shaped, rectified) to vestibular versus proprioceptive stimulation Figure 2—figure supplement 3).

Purkinje cell responses to simultaneous proprioceptive and vestibular stimulation

So far, we have shown that most Purkinje cells in our population were sensitive to neck proprioceptive as well as vestibular stimulation, and that we categorized these neurons as ‘bimodal’ versus neurons that were only responsive to vestibular stimulation as ‘unimodal’. The vestibular sensitivities of bimodal Purkinje cells were comparable to those of their unimodal counterparts ($p = 0.17$). We further found that the neck sensitivities of bimodal neurons were most often (67%) antagonistic relative to their vestibular sensitivities in the preferred direction. This can be seen in Figures 3A,B, where the average vectors representing the neuronal response to the vestibular and proprioceptive stimulation point in opposite directions (Figs. 3A,B, thick blue versus green arrows, respectively). In contrast, relative to vestibular sensitivities in non-preferred direction bimodal cells were as likely to have antagonistic as agonistic responses to neck proprioceptive stimulation (Figure 3—figure supplement 1).

During everyday activities, we move our head relative to our body, and thus simultaneously activate both vestibular sensors and neck proprioceptors. To directly establish how vestibular and neck proprioceptive information is integrated in the anterior vermis, we next recorded the responses of the same Purkinje cell populations during combined stimulation of neck proprioceptors and the vestibular system. Specifically, we applied ipsilaterally and
contralaterally directed rotations of the monkey’s head relative to its earth-stationary body (i.e., head-on-body rotations; see METHODS), again with the same motion profiles as those used above in the assessment of neuronal vestibular and neck proprioceptive sensitivities. The responses of the same three example neurons above in Figures 1,2 are shown in Figure 3C. The head motion-based linear estimation of firing rate (solid black traces, see Methods) is plotted on the firing rate for each cell. A firing rate prediction (dashed red traces) based on the linear summation of each neuron’s sensitivity to vestibular and neck proprioceptive stimulation when each was applied in isolation (i.e., Figs. 1 and 2, respectively) is superimposed for comparison. The example neurons were typical in that each neuron’s modulation for combined stimulation in the preferred direction (i.e., grey columns) was well predicted by the linear summation of the neuron’s vestibular and proprioception sensitivities. The polar plots show the vector summation (dashed red arrow) of the example neuron’s response to vestibular and proprioceptive stimulation (blue and green arrows) when applied in isolation versus the response vector for combined stimulation (black arrow; Figure 3C-figure supplement 2). Correspondingly, there was good alignment between the vector length and direction computed for the firing rate estimate and prediction for these three example neurons for the head-on-body motion in the preferred direction.

Figure 3D,E summarizes the population data for unimodal and bimodal Purkinje cells in each of the three stimulation conditions. Average response sensitivities are shown for preferred (Fig. 3D) and non-preferred (Fig. 3E) direction motion. Note that since there were no significant differences between the response of Type I and II cells (other than their preferred direction) we reported the responses of both groups together, by accounting for the difference in the direction of the modulation of Type II cells. We first hypothesized that the vestibular sensitivity of unimodal neurons should remain constant across conditions regardless of whether the neck proprioceptors were stimulated. Consistent with this proposal, we found that unimodal cell response sensitivities (open bars) were comparable during the vestibular-only and combined stimulation conditions (Figs. 3D, E, p >0.22). Likewise, response phases of unimodal neurons were comparable for both conditions (preferred: 11±5 versus 11±14; p=0.21; vs. non-preferred: 27±8 versus 14±18; p=0.77). In contrast, we hypothesized that since the vestibular and proprioceptive sensitivities of bimodal Purkinje cells were generally antagonist (i.e., Fig. 3A, Figure 3—figure supplement 1), the oppositely modulated inputs from neck proprioceptors should effectively suppress the vestibular driven responses during the combined conditions. Indeed, consistent with this prediction, the sensitivities of bimodal Purkinje cells were reduced during the combined stimulation condition relative to the vestibular-only condition (Figs. 3D,E, filled bars, p <0.027).

Above, we showed that the responses of our three example neurons in the combined stimulation were well predicted by the linear summation of the neuron’s vestibular and proprioception sensitivities applied in isolation, particularly for stimulation in the preferred direction. We next explicitly addressed whether this simple linear model of vestibular-proprioceptive integration could reliably predict neuronal responses in the combined condition...
across our population of Purkinje cells. To do this, we compared on a neuron-by-neuron basis
and estimated and predicted head-on-body rotation sensitivities (Fig. 4A) and phases (Fig. 4B)
for all the Purkinje cells in our sample. Overall, estimated and predicted sensitivities and phases
were comparable \( (R^2 = 0.77 \) and 0.75 for sensitivity and phase, respectively, \( p<0.001 \)). The
similarity between values is shown by the slope of the line fits to the data which were not
different from 1 \( (p = 0.42 \) and 0.83 for gain and phase, respectively). Thus, the summation
model provided a good estimate of the gain of the preferred direction responses during
combined stimulation. Similar results were obtained in our analysis of the non-preferred
direction responses (Figure 4—figure supplement 1).

As stated above, the generation of vestibulospinal reflexes requires central pathways to
explicitly transform vestibular information from a head-centered to a body-centered reference
frame during self-motion. To better understand the coding by our population of neurons, we first
computed a "head sensitivity" and a "body sensitivity" ratio for each neuron (Fig. 5A, see
Methods). Two theoretical neurons, one that selectively encodes head-in-space and the other
that selectively encodes body movement are indicated by red and orange stars respectively. A
neuron selectively encoding head-in-space motion (red star) would display comparable
responses to whole-body and head-on-body rotations (head sensitivity ratio= 1), while not
responding to body-under-head rotations (body sensitivity ratio= 0). On the other hand, a
neuron selectively encoding body motion would display a comparable response to whole-body
and body-under-head rotations (orange star, body sensitivity ratio= 1), while not responding to
head-on-body rotations (head sensitivity ratio= 0). In contrast, comparison of these ratios across
each of the Purkinje cells in our neuronal population revealed considerable heterogeneity in the
relationship between these two measures relative to these theoretical neurons. As reviewed
above, anterior vermis Purkinje cells target neurons in the deep cerebellar nuclei (i.e., rFN)
(Batton et al., 1977; Yamada and Noda 1987). Thus, for comparison, we computed these ratios
for rFN neurons that had been studied during the same conditions (Brooks and Cullen, 2009).
The red and orange shaded areas represent the distribution of our sensitivity ratios for the
unimodal and bimodal rFN neuron populations reported in this prior study. Notably, in contrast
to the Purkinje cells of our present study, the relationship between the rFN unimodal and
bimodal neuron sensitivity ratios are well-aligned with that of our theoretical neurons that
selectively encoded head and body movement, respectively.

To next evaluate the transformation of vestibular information from a head-centered to body-
centered reference frame during self-motion for each Purkinje cell we computed a coding index
(see Methods). Specifically, this index compared each neuron's sensitivity when only the head
moved relative to space (i.e., head-on-body rotation, Fig. 3) versus when only the body moved
relative to space (i.e., body-under-head rotation, Fig. 2), to the combined stimulation condition.
The results from the analysis of our Purkinje cell population are shown in Figure 5B. Indeed,
only a minority of neurons were designated as primarily head (26%) or body (2%) encoding
(light and dark orange bars, respectively). A complementary analysis of non-preferred direction
responses (relative to vestibular stimulation) revealed similar results (Fig. 5—figure
supplement 1). Again, for comparison, the corresponding distribution of coding indices estimated for rFN neurons from Brooks et al. 2009 is shown for comparison (Figure 5B, top right inset). In contrast to Purkinje cells the majority of neurons were designated as primarily head (34%) or body (26%) encoding.

Influence of head position on Purkinje cell vestibular responses

In theoretical models of reference frame transformations, responses to the sensory inputs are generally modulated by a postural signal (e.g., the position of the head relative to the body) (Pouget and Snyder, 2000, Salinas 2001). Indeed, neurons in the deep cerebellar nuclei of primates show such tuning. Specifically, the vestibular responses of bimodal neurons in the rostral fastigial nucleus modulate as a function of head position (Brooks and Cullen 2009; Kleine et al., 2004; Shaikh et al., 2004)). This finding has been taken as support for the view that a reference frame transformation of vestibular signals from head- to body-centered occurs in the cerebellar vermis (reviewed in Cullen 2019). Thus, we next asked: How is this tuning generated? And more specifically, is it computed within the deep cerebellar nuclei or instead inherited from the Purkinje cells that target neurons in the deep cerebellar nuclei? To address these questions, we first determined whether the vestibular responses of Purkinje cells were affected by static changes in head-on-body position (i.e., “gain field” condition, see METHODS).

We measured neuronal responses to vestibular stimulation (i.e., whole-body rotation) applied with the head positioned at 5 different orientations ranging from −30 (left) to +30° (right) relative to the body (−30, −15, 0, 15, and 30°). The example bimodal neuron was typical in that it displayed marked changes in vestibular sensitivity with changes in head-on-body position (Fig. 6A). In contrast, we did not find evidence for such tuning in unimodal neurons (Fig. 6B).

To quantify each Purkinje cell’s tuning we fit a Gaussian function to vestibular sensitivity as a function of head position (see Methods), and computed the tuning width, amplitude, and mean direction provided by the best fit to each neuron (Fig. 6C, top row; filled and open blue bars denote bimodal and unimodal neurons (N = 13 vs 4, respectively). Note that the small number of unimodal neurons tested in this condition reflects that they constituted a relatively small percentage of our overall Purkinje cell population. First, bimodal neurons were more narrowly tuned than were unimodal neurons (mean tuning widths; 7.2 vs. 15°, respectively). Additionally, bimodal neurons showed stronger tuning relative to unimodal neurons (mean tuning amplitude; 0.52 vs. 0.05 (sp/s)/(deg/s), respectively. Finally, there was no difference in the mean of the tuning curve between unimodal neurons and bimodal neurons (p > 0.37). We next compared the tuning of our bimodal and unimodal Purkinje cells with that previously described for their target neurons in the rFN (Brooks and Cullen, 2009). The corresponding distributions of rFN neuron tuning width, amplitude, and mean direction are plotted in the bottom row of Fig. 6C. To facilitate comparison between the tuning of Purkinje and rFN cells, we aligned the peak of each individual neuron’s tuning curve with zero and averaged the resultant curves across bimodal
and unimodal groups for each (Fig. 6D). Overall, the strength of tuning was significantly higher for bimodal rFN than Purkinje cells (Fig. 6D compare solid gray and black lines, ~30% reduction for Purkinje cells, p<0.001). Tuning width was also reduced for bimodal Purkinje cells (~40% reduction), while mean tuning direction was comparable for both cell groups (p > 0.05). Moreover, tuning was consistently stronger for bimodal than unimodal neurons in Purkinje cells as has previously been shown for rFN neurons (Fig. 6D, compare solid and dashed lines). We note that because the interaction between vestibular responses and head-on-body position that underlies the tuning shown in Fig. 6 is inherently nonlinear, this tuning cannot be predicted by the component of the Purkinje cells’ dynamic modulation that is in phase with head position during body-under-head rotation (i.e., Fig. 2A).

**Linear combination of the Purkinje cells’ response can encode head and body motion**

To summarize, our results have shown that while most vestibular-sensitive Purkinje cells in the anterior vermis integrate vestibular and neck proprioceptive signals, the transformation from head- to body-centered reference frame is not complete. Instead, single bimodal Purkinje cells generally dynamically encoded intermediate representations of self-motion that were between head and body motion. In contrast, bimodal neurons in the deep cerebellar nuclei - the primary target of these Purkinje cells (Fig. 7A; rostral fastigial nucleus) - dynamically encode body motion (i.e., orange shaded region, Fig. 5C) and also show stronger vestibular tuning as a function of head-on-body-position. Thus, taken together, our present results suggest that the transformation from a head- to body-centered representation of self-motion is achieved by integrating the activities of multiple Purkinje cells.

Accordingly, we next tested this hypothesis. Specifically, to quantify the actual number of Purkinje cells necessary to explain the responses of bimodal rFN neurons, we determined whether a simple linear model optimizing the weights of the activities of multiple Purkinje cells (see Methods) could generate bimodal rFN neural responses across conditions (Fig. 7B). As expected, combining the activities of more Purkinje cells (i.e., increasing population size) led to an increase in the goodness of fit (Fig. 7C). Data sets used for this modeling first included Purkinje cell responses recorded during (i) our three dynamic conditions (i.e., whole-body, body-under-head, head-on-body rotations) alone (black curve), and (ii) these same three dynamic conditions as well as the the gain field condition (i.e., Fig. 6; dashed blue curve). In the latter case, the tuning of Purkinje cells that were not held long enough to test during gain-field paradigm were generated from the tuning curves distribution of the tested neurons (see METHODS). Importantly, in both cases we found that the weighted activities of ~40 neurons generated responses that well approximated those previously reported for bimodal rFN neurons (Fig. 7C, red arrow); the confidence intervals our model estimates that of the rFN neural responses completely overlapped for a population of ~40 neurons. Thus, a population of 40 Purkinje cells could explain the dynamic representation of body motion across conditions (Fig. 7D), as well as robust encoding of vestibular stimuli as a function of static head position observed in bimodal rFN neurons (Fig. 7D, right panel).
Above we described how Purkinje cells demonstrate considerable heterogeneity in their responses to both vestibular and proprioceptive stimulation. Thus, we next asked whether certain Purkinje cell classes were weighted higher in our population model than others. For example, given that rFN neurons show linear tuning, one might predict that Purkinje cells with linear tuning might be weighted higher in our population model than those with v-shaped tuning. However, we found that this was not the case. The model weight distributions were similar for linear versus v-shaped versus rectifying Purkinje cells. Similarly, model weight distributions were similar for (i) bimodal vs. unimodal Purkinje cells, (ii) Type I vs. Type II Purkinje cells, as well as (iii) Purkinje cells with agonistic vs. antagonistic vestibular and proprioceptive responses. These distributions are illustrated in Fig. 7-figure supplements 1&2 for our modeling of bimodal versus unimodal rFN neurons, respectively.

Finally, we note that our simple population model above in Fig. 7A assumed no input to the rFN neurons other than that from Purkinje cells. However, the fastigial nucleus receives mossy fiber inputs via the vestibular nuclei, reticular formation, and central cervical nucleus (reviewed in Voogd et al. 1996) that likely also encode vestibular and/or neck proprioceptive information (e.g., Roy and Cullen 2001, Kubin et al., 1990, 1981; Thomson et al. 1996). Therefore, we next tested the effect of adding simulated mossy fiber inputs to our model. Prior studies have shown that the dynamics of responses of vestibular nuclei neurons strongly resemble those of unimodal fastigial neurons in rhesus monkeys (i.e., they encode vestibular input and are insensitive to neck proprioceptive inputs, Roy & Cullen, 2001). In contrast, the response of neurons in the reticular formation and central cervical nucleus to such yaw head and/or neck rotations have not yet been described. We therefore simulated mossy fiber input first as a summation of vestibular and neck proprioceptive inputs, for which the gains and phases were randomly drawn from a distribution, comparable to that previously reported (Mitchell et al. 2017) in the vestibular nuclei (see Methods). We repeated this approach for a total of 1000 simulations (Fig. 7-figure supplement 3). We then further explored the effect of systematically altering this simulated mossy fiber input relative to the reference distribution of mossy fiber inputs by i) doubling the gain, ii) reducing the gain by half, iii) doubling the phase, and iv) reducing the phase by half (Fig. 7-figure supplement 4). Overall, we found that the addition of such simulated mossy fiber inputs did not dramatically alter our estimate of the Purkinje cell population size required to generate rFN neurons responses (~50 versus 40; Fig. 7-figure supplement 3&4). Furthermore, comparable results were obtained for model weight distributions as shown above in Fig. 7-figure supplements 1&2.

Finally, for completeness, we also used the same approach to quantify the number of Purkinje cells necessary to explain the responses of unimodal rFN neurons and obtained comparable results (Fig. 7—figure supplement 5). Interestingly, our finding that a population of ~40-50 Purkinje cells is again required to explain the responses of bimodal and unimodal rFN neurons matches the value established independently from anatomical studies of Purkinje cell - deep cerebellar nucleus neuron projection ratio. We further consider this point below in the Discussion.
Discussion

Summary of results

Here we recorded the simple spike activity of Purkinje cells of the anterior vermis during passive vestibular (i.e., whole-body rotation), neck proprioceptive (i.e., body-under-head rotation), and a combination of vestibular and neck proprioceptive stimulation (i.e., head-on-body rotation). First, we found that most Purkinje cells responded to both vestibular and neck proprioceptive stimulation (i.e., bimodal neurons). Second, the linear combination of the responses to dynamic neck proprioceptive and vestibular stimulation alone provided a good estimate of each Purkinje cell’s response during combined stimulation. Third, bimodal neurons generally did not encode either the motion of the head or body in space across conditions. Instead, they dynamically encoded intermediate representations of self-motion between head and body motion. Additionally, bimodal neurons, but not unimodal neurons, showed tuning for the encoding of vestibular stimuli as a function of static head position. Finally, using a simple linear population model, we establish that combining inhibitory responses from ~40-50 Purkinje cells can explain the responses of target neurons in deep cerebellar nuclei across all self-movement conditions. Thus, our findings in alert monkeys provide new insight into the neural mechanisms underlying the coordinate transformation by which the cerebellum uses neck proprioceptive information to transform vestibular signals from a head- to body-centered reference frame.

Purkinje cells have diverse temporal responses to dynamic vestibular and neck proprioceptive sensory stimulation

The integration of vestibular and neck proprioceptive-related information is required to convert head-centered vestibular signals to the body-centered reference frame required for postural control (reviewed in Cullen 2019). Our recordings in the anterior vermis of alert monkeys demonstrate that most vestibular sensitive Purkinje cells also encode neck proprioceptive-related information. As reviewed above, anterior vermis Purkinje cells project to the rostral fastigial nucleus (rFN), the most medial of the deep cerebellar nuclei (Fujita et al. 2020, Husson et al. 2014) which plays a key role in the control of posture. Two types of rFN neurons have been previously identified in alert monkeys: unimodal and bimodal neurons (Brooks and Cullen 2009). Unimodal neurons respond to vestibular stimulation during passive rotations and dynamically encode head movement. Bimodal rFN neurons respond to both vestibular and neck proprioceptive stimulation and dynamically encode body movement. Notably, because the vestibular and neck proprioceptive sensitivities of rFN bimodal neurons are both equal and complementary in sign, they sum linearly to effectively cancel each other during passive head-on-body rotations - a condition in which both sensory systems are activated but the body does not move in space. In contrast, here we found that vestibular-sensitive anterior vermis Purkinje cells were on average more sensitive to vestibular than proprioceptive stimulation and that there was considerable variability in the relative signs of responses to each modality. As a result,
cancellation of these two inputs during passive head-on-body rotations was the exception rather than the rule (i.e., Figure 3B) with the vast majority of bimodal Purkinje cells demonstrating significant modulation in response to passively applied head-on-body rotations. Thus, unlike bimodal rFN neurons, which dynamically encode body motion, bimodal Purkinje cells dynamically encode an intermediate representation of self-motion.

Reference frame transformations: Purkinje cell vestibular responses modulated by posture

Theoretical models of reference frame transformations commonly include a sensory input (e.g., vestibular or visual information) that is modulated by a postural signal (e.g., head-on-body position) (Pouget and Snyder 2000; Salinas 2001). The resultant modulation of the sensory signal is commonly referred to as a gain field (Andersen and Mountcastle 1983) and is thought to be mediated via nonlinear interactions between sensory responses and head/body referenced cues (Zipser and Andersen, 1988; Salinas 2001). Our present results reveal the neural substrate of such a reference frame transformation required for postural control. Notably, bimodal anterior vermis Purkinje cells displayed vestibular tuning as a function of head-on-body position during horizontal rotations. This tuning is similar but not as strong as that shown by downstream bimodal neurons in the target rFN (Brooks and Cullen 2009), and indeed some rFN neurons do encode vestibular information in a body-centered reference frame for both two dimensional (Kleine et al., 2004; Shaikh et al., 2004) and three dimensional (Green et al. 2018) self-motion. Thus, our present data establish that the modulation of vestibular information by a postural signal becomes more marked in the progression from the cerebellar cortex to the deep cerebellar nuclei. Interestingly, in the present study, such nonlinear interactions between neck position and vestibular signals were only in bimodal and not unimodal vestibular Purkinje cells. Future experiments are required to understand the implications of the dynamic coding head rather than body movements by the unimodal neurons.

Finally, it is noteworthy that our findings regarding the transformation from a vestibular to head-centered reference frame in the anterior vermis of the alert primate contrast with those of Pompeiano, Manzoni, and colleagues in anesthetized decerebrate cats. Using dynamic tilt stimuli, they concluded that the direction of average response vector of Purkinje cells encoding both vestibular and proprioceptive information well corresponded to body tilt – consistent with a complete transformation from head- to body-centered reference frame (Denoth et al., 1979, Manzoni et al., 1998; 2004). One potential explanation for this apparent difference in neural strategy is that our studies were performed in intact alert behaving animals whereas Manzoni and colleagues completed their experiments in anesthetized decerebrate preparation where modulation/gating by cortical structures is not present. Additionally, there are significant differences across species regarding how the vestibular system integrates multimodal information even at the first stage of central processing in the vestibular nuclei (reviewed in Cullen 2019). For instance, vestibular nuclei neurons in alert mice, cats, and cynomolgus monkeys commonly display vestibular–proprioceptive convergence (Medea and Cullen 2013;
In contrast, in rhesus monkeys, vestibular nuclei neurons are only sensitive to vestibular input, and instead, proprioceptive information is integrated only at the subsequent levels of vestibular processing, most notably in the deep nuclei of the cerebellum (Roy and Cullen 2001; Brooks and Cullen 2009; Carriot et al., 2013).

Population coding: the heterogeneous response of Purkinje cells and convergence in the rFN

Our results establish that there is considerable heterogeneity in the response dynamics of anterior vermis Purkinje cells to vestibular and/or neck proprioceptive sensory stimulation. Semicircular canal afferents and vestibular nuclei neurons provide the primary source of vestibular information to the cerebellum via mossy fiber input. However, while they encode head velocity with a phase lead, the responses of individual Purkinje cells actually more often lagged rather than led head velocity. Albus and Marr proposed that the divergent feedforward mossy fiber projections onto a far larger number of granule cells effectively expand the dimensionality of neural space, in turn allowing better downstream decoding to linearly classify dynamic patterns of activity (Marr 1969; Albus, 1971). Indeed, recent studies have shown that mossy fibers from multiple sensory systems converge on each of more than 50 billion granule cells (Chabrol et al., 2015, Knogler et al. 2017, Lanore et al., 2021), with interneurons likely further contributing to the temporal diversity of granule cell responses (Rousseau, 2012; Kennedy et al. 2014). In turn, > 100,000 granule cells project to a single Purkinje cell via parallel fibers (Fujishima et al., 2018). Thus, together these features of the cerebellar microcircuitry are well designed to generate high-dimensional dynamic coding of information by Purkinje cells relative to their mossy fiber input across regions of the cerebellum including the anterior vermis.

In this context, the heterogeneity we observed in anterior vermis Purkinje cells responses then contrasts strikingly with the responses of their target neurons in rFN (Brooks and Cullen, 2009). Our estimation that pooling the responses of a population of ~40-50 Purkinje cells can explain more homogeneous responses of bimodal and unimodal rFN neurons matches that established independently from anatomical studies of the Purkinje cell-deep cerebellar nucleus neuron projection ratio in rodents and cats (Person and Raman 2012; Palkovits et al., 1977). Additionally, these Purkinje cells likely send direct projections to the vestibular nuclei. Testing with comparable stimulation protocols has established that the responses of vestibular nuclei neurons are comparable to those of unimodal rFN neurons (compare Brooks and Cullen, 2019 with Brooks and Cullen, 2016). Thus, our present modeling results regarding the population convergence required to account for unimodal rFN neurons can be directly applied to vestibular nuclei neurons. Interestingly, Purkinje cells can display patterns of neuronal synchrony during active movements (Person and Raman 2012; Sarnaik and Raman2018; Wu and Raman 2017) which could, in turn, alter the timing and modulation of target neuron responses in the deep cerebellar nuclei in a non-linear manner. Nevertheless, we found that responses could be predicted using a simple linearly weighted summation of ~40-50 neurons. In this context, we note our modeling was based on averaged Purkinje cell and rFN neuron responses. Future
studies including simultaneous recordings from Purkinje cells and rFN neurons can provide additional insight into whether comparable population sizes can account for single trial responses in real-time.

Finally, it is noteworthy that our study focused on the sensory responses of Purkinje cells (i.e., responses to vestibular and/or proprioceptive stimulation) during passively applied self-motion. Prior studies focused on the responses of Purkinje cells during voluntary movements have similarly concluded that they are more heterogeneous than those of their target neurons in the deep cerebellar nuclei (e.g., saccades: Thier et al., 2000; wrist control: Tomatsu et al., 2016). Interestingly, in their analysis, Tanaka et al. (2019) likewise estimated that linearly pooling the responses of ~40-50 Purkinje cells could account for the more homogeneous responses of target neurons in the deep cerebellar nucleus (i.e., the dentate nucleus) during voluntary wrist movements. We speculate that expanded dimensionality of the cerebellum provides a basis set for sensorimotor errors as well as plasticity at the level of Purkinje cells required to generate accurate movements (reviewed in Sohn et al. 2020) as well as ensure robust calibration over time. Overall, our current results reveal a striking transformation from heterogeneous response dynamics of cerebellar Purkinje cells to more stereotyped response dynamics of neurons in the targeted deep cerebellar nucleus. These findings provide new insights into the neural computations that ultimately ensure accurate postural control in our daily lives.
Methods

Experimental Model and Subject Details
Animal experimentation: All experimental protocols were approved by the Johns Hopkins University Animal Care and Use Committee and were in compliance with the guidelines of the United States National of Health (PR19M408). The cerebellar recordings were conducted in two male macaque monkeys (Macaca mulatta). The animals were housed on a 12-hour light/dark cycle. The recording sessions were about three times a week, for approximately two hours each session. Both animals had participated in previous studies in our laboratory, but they were in good health condition and did not require any medication.

Method Details
Surgical Procedures
The two animals were prepared for chronic extracellular recording using aseptic surgical techniques described previously (Massot et al., 2012). Briefly, animals were pre-anaesthetized with ketamine hydrochloride (15 mg/kg im) and injected with buprenorphine (0.01 mg/kg im) and diazepam (1 mg/kg im) to provide analgesia and muscle relaxation, respectively. Loading doses of dexamethasone (1 mg/kg im) and cefazolin (50 mg/kg iv) were administered to minimize swelling and prevent infection, respectively. Anticholinergic glycopyrrolate (0.005 mg/kg im) was also preoperatively injected to stabilize heart rate and to reduce salivation, and then again, every 2.5–3 h during surgery. During surgery, anesthesia was maintained using isoflurane gas (0.8%–1.5%), combined with a minimum 3 l/min (dose adjusted to effect) of 100% oxygen. Heart rate, blood pressure, respiration, and body temperature were monitored throughout the procedure. During the surgical procedure, a stainless-steel post for head immobilization and recording chambers were fastened to each animal's skull with stainless-steel screws and dental acrylic. Craniotomy was performed within the recording chamber to allow electrode access to the cerebellar cortex. An 18-mm-diameter eye coil (three loops of Teflon-coated stainless-steel wire) was implanted in one eye behind the conjunctiva. Following surgery, we continued dexamethasone (0.5 mg/kg im; for 4 days), anafen (2 mg/kg day one, 1 mg/kg on subsequent days), and buprenorphine (0.01 mg/kg im; every 12 h for 2–5 days, depending on the animal's pain level). In addition, cefazolin (25 mg/kg) was injected twice daily for 10 days. Animals recovered in 2 weeks before any experimenting began.

Data acquisition:
During the experiments, the monkey sat in a primate chair secured to a turntable, and its head was centered in a coil system (CNC Engineering). Extracellular single-unit activity was recorded using enamel-insulated tungsten microelectrodes (Frederick-Haer). The location of the anterior vermis of the cerebellar cortex was determined relative to the abducens nucleus identified based on stereotypical neuronal responses during eye movements. The Purkinje cells were identified by their characteristic complex spike activity. The angular velocity of the turntable was measured using a gyroscope sensor (Watson Industries, Eau Claire, Wisconsin). Monkeys'
gaze and head angular positions were measured using the magnetic search coil technique. The neck torque produced by the monkey against its head restraint was measured using a reaction torque transducer (QWFK-8M; Honeywell, Canton, MA). All analog behavioral signals were low-pass filtered with a 125Hz cut-off frequency and acquired at 1 kHz. The neural activity was recorded at 30kHz using a data acquisition system (Blackrock Microsystems). Action potentials from the neural recording were sorted using a custom Matlab GUI (MathWorks), which provides threshold, clustering, and manual selection/removal methods.

**Head and Body motion paradigms:**

Two monkeys were trained to follow a target projected onto a cylindrical screen located 60 cm away from the monkey's head. Each neuron’s insensitivity to saccades and ocular fixation was confirmed by having the head-restrained monkey attend to a target that stepped between horizontal positions over a range of ±30°. Each neuron’s lack of response to eye movements was further confirmed by absent responses to smooth pursuit eye movements during sinusoidal target motion (0.5 Hz, 40°/s peak velocity).

Next, to characterize each Purkinje cell’s vestibular and proprioceptive sensitivities, we applied rotational stimuli mimicking the monkey’s head movement generated during ±30 deg orienting gaze shifts in the head-unrestrained condition (i.e., “active-like” condition). Use of this head movement trajectory facilitates direct comparison with rFN and vestibular nuclei neurons (e.g., Brooks et al., 2015). First, vestibular sensitivities were assessed by applying whole-body rotations about an earth-vertical axis in the dark (i.e., whole-body-rotations). Second, neck proprioceptive sensitivities were assessed by rotating the monkey's body with this same active-like trajectory while its head was held stationary relative to space (i.e., body-under-head rotations). Third, neural sensitivities to combined proprioceptive and vestibular stimulation were assessed by passively rotating the monkey's head relative to its stationary body (i.e., head-on-body rotations) with this same trajectory. Finally, in a subset of neurons, we also applied whole-body rotations about an earth-vertical axis in the dark (1Hz, ± 40˚/s) with the head statically oriented at five different positions relative to the body (-30, -15, 0, 15, and 30 degs) to assess whether static neck position influenced vestibular-induced modulation during whole-body sinusoidal rotation (i.e., the ‘gain field’ condition).

Histological analysis confirmed the Purkinje cells were located in lobules II-V of the anterior vermis, ~0 to 2 mm from the midline. We note that while we first tested the vestibular sensitivity of individual neurons, we did also test whether neurons that were insensitive to vestibular stimulation responded to neck proprioceptive stimulation. Consistent with Manzoni and colleagues’ prior studies in anesthetized cat (12%, Manzoni et al. 1998) we found that only a small portion of Purkinje cells (~10%) fell into this latter category.
Data analysis:

Analysis of neuronal discharge dynamics: Data were imported into the Matlab (The MathWorks) programming environment for analysis, filtering, and processing as previously described (Dale and Cullen, 2017). Neuronal firing rate was computed by filtering spike trains with a Kaiser window at twice the frequency range of the stimulus (Cherif et al. 2008). We first verified that each neuron neither paused nor burst during saccades and was unresponsive to changes in eye position during fixation. We then used a least-squares regression analysis to describe each Purkinje cell simple spike’s response to whole-body and body-under-head rotations:

\[
\hat{f}(t) = b + c_{p,i}X_i(t) + c_{v,i}\dot{X}_i(t) + c_{a,i}\ddot{X}_i(t)
\]

(1)

where \(\hat{f}(t)\) is the estimated firing rate, \(b\) is a bias term, \(c_{p,i}\), \(c_{v,i}\), and \(c_{a,i}\) are coefficients representing the position, velocity, and acceleration sensitivities respectively to head (\(i = 1\)) or body motion (\(i = 2\)), and \(X_i\), \(\dot{X}_i\), and \(\ddot{X}_i\) are head (\(i = 1\)) or body (\(i = 2\)) position, velocity and acceleration (during whole-body and body-under-head rotations), respectively. This least-squares regression was solved for non-negative and non-positive criterion to ensure sign consistency across estimated coefficients. For each model coefficient in the analysis, we computed 95% confidence intervals using a nonparametric bootstrap approach (n=2000; Carpenter and Bithell, 2000, Sylvestre and Cullen 1999). All non-significant coefficients were set to zero. We then used coefficients to estimate the sensitivity and phase of the response using the following equations:

\[
\text{Sensitivity} = \text{sgn}(c_{p,i}, c_{v,i}, c_{p,i}) \times \sqrt{\frac{(2\pi f)^2 c_{a,i} - c_{p,i})^2}{(2\pi f)^2} + (2\pi f c_{v,i})^2}
\]

(2)

\[
\text{Phase} = \tan^{-1}\left(\frac{(2\pi f)^2 c_{a,i} - c_{p,i}}{2\pi f c_{v,i}}\right)
\]

(3)

For which \(f = 1Hz\) to match the duration of half-cycle of movements (500ms) and the sign term (i.e., \(\text{sgn}(c_{p,i}, c_{v,i}, c_{p,i})\)) equals either 1 or -1 for positive versus negative coefficients, respectively. The sensitivity of the Purkinje cells to the neck proprioceptive stimulation (during body-under-head rotations) was used to categorize the cells into unimodal (zero sensitivity) and bimodal (non-zero sensitivity).

Neuronal tuning to vestibular and proprioceptive inputs was further categorized as linear, rectifying, or V-shaped. Linear neurons demonstrated increased and decreased firing rates in the preferred and non-preferred directions, respectively. The difference between the magnitude of sensitivities in each of the two directions was within 0.2 (sp/s)/(deg/s). Rectifying neurons demonstrated increased firing rate in the preferred direction and minimal modulation (i.e.,
sensitivity smaller than 0.2 (sp/s)/(deg/s)) in the non-preferred direction. V-shaped neurons demonstrated an increased firing rate in both directions. The difference between the magnitude of their sensitivities in each of the two directions was within 0.2 (sp/s)/(deg/s). Finally, neurons that did not fit any of these criteria were characterized as ‘other’. Note that V-shaped neurons were categorized as type I or II based on the direction for which their vestibular sensitivity was larger, since their responses in each direction were not identical.

We used a similar approach to estimate sensitivities to passive head-on-body movements. Since in this condition, it is not possible to dissociate neck proprioceptive and vestibular sensitivities, we estimated them as a single coefficient. Estimated sensitivities were compared to those predicted from the linear summation of the vestibular and proprioceptive sensitivities estimated for the same neuron during passive whole-body and body-under-head rotations (termed summation model), respectively. To quantify the ability of the linear regression analysis to model neuronal discharges, the variance-accounted-for (VAF) for each regression equation was determined as previously described (Cullen et al., 1996). Values are expressed as mean ± SD and paired-sample Student’s t-tests were used to assess differences between conditions.

**Quantifying head versus body encoding:** We computed a ‘head sensitivity ratio’ and ‘body sensitivity ratio’ for each Purkinje cell. These ratios were defined as the neuron’s (i) sensitivity to head-on-body rotation/sensitivity to whole-body rotation, and (ii) sensitivity to body-under-head rotation/sensitivity to whole-body rotation, respectively. Further to quantify the relative encoding of head versus body motion by a given cell, we computed a ‘coding index’, which was defined as the ratio (smaller value)/(larger value) of these two ratios.

**Quantification of head position on Purkinje cell vestibular sensitivity:** The tuning curves for different head-on-body positions were fit with Gaussian curves with the following equation:

\[
S = Ae^{-(\mu_{\text{position}} - \mu)^2 / 2\sigma^2}
\]

(4)

Where \(\mu\) represents the mean, \(\sigma\) is a measure of the width, and \(A\) is the amplitude from the peak to the base of the Gaussian curve (as described previously, Brooks and Cullen, 2013).

**Population modeling of Purkinje cells:** To determine whether integrating the activities of multiple Purkinje cells could explain the response of their target neurons in the rFN, we used the linear model below:

\[
rFN = \sum_{i=1}^{N} w_i \times Pcell_i
\]

(5)

where \(rFN\) is a reconstructed firing rate response of an rFN neuron. The \(w_i\) corresponds to weights of connection from Purkinje cells to an rFN neuron, which all considered non-positive to reflect inhibitory synapses from Purkinje cells to rFN neurons. \(Pcell_i\) are observed firing rate of
simple spikes $N$ Purkinje cells, where $N$ is a number between 1 and the total number of Purkinje
cells in the dataset. For each $N$ we used a bootstrapping approach to find the 95% confidence
intervals of the goodness of fit ($R^2$) as well as the model predictions.

To model the population response of Purkinje cells during the “gain-field condition”, we first fit a
gaussian function of the tuning curve of 13 bimodal Purkinje cells that were recorded during this
condition. Next, we used the parameters of these gaussian functions to find a normal
distribution representing the tuning curves of bimodal Purkinje cells. Then for the remaining
Purkinje cells that were not recorded during the “gain-field” condition, we generated tuning
curves by drawing from this normal distribution. Since 4 unimodal Purkinje cells that were
recorded during the “gain-field” condition did not demonstrate significant tuning, we did not
consider any tuning to the remaining unimodal Purkinje cells.

Finally, we modeled the contribution of the mossy fiber input to the rFN as a summation of
independent responses to vestibular and neck proprioceptive stimulation. To simulate the
mossy fiber input, we randomly selected response gains and phases from normal distributions
that described the responses of neurons in the vestibular nuclei (i.e., 0.6±0.1 (sp/s)/(deg/s) and
20±5 deg, respectively), and repeated this for a total of 1000 simulations. We further assessed
the robustness of our modeling performance by modifying these distributions. Specifically, we
tested the effect of either doubling or halving the gain (i.e., 1.2±0.2 and 0.3±0.05 (sp/s)/(deg/s)),
respectively) or phase (i.e., 40±10 and 10±2.5 deg, respectively), resulting simulations based on
four modifications of the original distribution.


Brooks JX, Cullen KE. 2014. Early vestibular processing does not discriminate active from passive self-motion if there is a discrepancy between predicted and actual proprioceptive feedback. Journal of Neurophysiology 111:2465–2478. doi:10.1152/jn.00600.2013


Figure captions

Figure 1 - Purkinje cell simple spike responses to vestibular stimulation. (A) Vestibular stimulation was generated by applying passive whole-body rotations about the vertical axis. The resulting neural responses are shown for three example Purkinje cells. The top two rows illustrate rotational head and body velocities. The bottom row shows the simple spike firing rate (gray shaded regions) with the linear estimation of the firing rate based on head motion superimposed (blue traces). The heat maps show the simple spike firing rate for individual trials. Insets: the relationship between simple spike firing rate (phase-corrected) and angular head-in-space velocity. (B, C) Distribution of vestibular sensitivities for motion in the preferred (B) direction (i.e., the direction resulting in the larger increase in simple spike firing rate) and non-preferred (C) direction. The dashed lines are fits on the distributions. Note, by convention positive and negative values in (B) represent cells with Type I versus II vestibular responses (i.e., preferred direction was ipsilateral versus contralateral, respectively). Insets: polar plots where the vector length and angle represent each neuron’s vestibular response sensitivity and phase, respectively. Filled and open arrows represent the population-averaged vectors for Type I and II cells, respectively.

Figure 2 - Purkinje cell simple spike responses to neck proprioceptive stimulation. (A) Proprioceptive stimulation was generated by applying body under head rotation about the vertical axis while holding the head earth. The resulting neural responses are illustrated for the same three example Purkinje cells shown above in Fig. 1. The top two rows illustrate rotational head and body velocities. The bottom row shows the resultant simple spike firing rate (gray shaded regions) with the linear estimation of the firing rate based on body motion superimposed (green traces). The heat maps show the simple spike firing rate for individual trials. Insets: the relationship between simple spike firing rate (phase-corrected) and angular body-in-space velocity. (B, C) Distribution of proprioceptive sensitivities for the preferred (B) and non-preferred (C) directions of body movement. Filled versus open bars represent neurons that were sensitive versus insensitive to neck proprioceptive stimulation (i.e., bimodal versus unimodal cells, respectively). The dashed lines are fits on the distributions. Insets: polar plots where the vector length and angle represent each neuron’s proprioceptive response sensitivity and phase, respectively. Filled versus open arrows represent the population-averaged vectors for neurons with Type I versus II vestibular responses (i.e., Fig. 1), respectively.

Figure 3 - Purkinje cells simple spike responses to combined vestibular–proprioceptive stimulation. (A, B) Polar plots illustrating the vestibular (blue) and neck proprioceptive (green) neuronal response sensitivities of Type I (A) and Type II (B) Purkinje cells for preferred direction of vestibular stimulation and complementary direction proprioceptive stimulation (i.e., body-under-head motion). Bold blue and green arrows represent the mean population vectors, respectively. Inset: scatter plots comparing the sensitivity of Type I (A) and Type II (B) Purkinje cells to vestibular and neck proprioceptive inputs. (C) Combined vestibular-proprioceptive stimulation was generated by applying passive head on body rotations about the vertical axis. The resulting neural responses are shown for the same three example Purkinje cells shown...
above in Figs. 1,2. The top two rows illustrate rotational head and body velocity. The bottom row shows the resultant simple spike firing rate (gray shaded regions). The linear estimation of firing rate based on head motion (solid black traces) and the firing rate prediction based on the linear summation of neck proprioceptive and vestibular sensitivities (dashed red traces) are both superimposed. Each neuron’s preferred motion direction for vestibular stimulation is indicated by the gray column. Polar plots (top) represent the sensitivity and phase of each neuron’s response to vestibular, proprioceptive, and combined stimulation as well as the response predicted by the summation model. (D, E) Bar plots comparing the sensitivities of bimodal and unimodal Purkinje cells to vestibular, proprioceptive, and combined stimulation in the preferred (D) and non-preferred (E) motion directions, as defined by each neuron’s responses to vestibular stimulation. The response sensitivities of Type I and II neurons are reported as positive values relative to ipsilaterally and contralaterally directed head movements, respectively, to facilitate comparison across all Purkinje cells.

Figure 4 – Purkinje cell simple spike responses to combined stimulation are well predicted by the linear summation of a given neuron’s responses to vestibular and proprioceptive stimulation when applied alone. (A,B) Comparison of estimated and predicted sensitivities (A) and phases (B) of Purkinje cell responses to head-on-body rotations in the preferred movement direction. The linear summation of a given neuron’s vestibular and neck proprioceptive sensitivities well predicts both sensitivity and phase measures in the combined condition. Blue lines and shading denote the mean ± 95% CI of linear fit.

Figure 5 – Heterogeneity in Purkinje cell simple spike encoding of head and body movement. (A) Scatter plot of the relationship between the head sensitivity ratio ($S_{\text{vest.}+\text{prop.}} / S_{\text{vest.}}$) and body sensitivity ratio ($S_{\text{prop.}} / S_{\text{vest.}}$) for the preferred direction. Histograms (top and right) illustrate the distributions of body and head sensitivity ratios, respectively. Orange versus red stars indicate ideal encoding of body versus head movement in space, respectively. For comparison, the red and orange shaded areas representing the distribution of values estimated for unimodal and bimodal rFN neurons (Brooks et al. 2009) are superimposed. Inset: examples of the responses of a bimodal (orange) and unimodal (red) rFN neurons during whole-body, body-under-head, and head-on-body movement is shown for comparison (Figure 5 A has been adapted from Figure Supplement 1 from Brooks and Cullen, 2013). (B) Distribution of coding indexes (see Methods). Positive and negative values correspond to agonistic and antagonistic responses to head vs. body encoding, respectively. Inset: the distribution of coding indices estimated for rFN neurons (Brooks et al. 2009) is shown for comparison.

Figure 6 – The vestibular responses of bimodal Purkinje cells show head-on-body position dependent tuning. (A, B) Tuning curves for the vestibular sensitivities of an example bimodal (A) and unimodal (B) Purkinje cell measured by applying whole-body rotation with the head oriented at different positions relative to the body. Note, bimodal neurons, but not unimodal neurons, show tuning as a function of head-on-body position. (C) Top panel: Distributions of tuning widths (left), amplitudes (middle), and means (right) for bimodal (filled
bars, N=13) and unimodal (open bars, N=4) Purkinje cells. Bottom panel: For comparison, the same distributions are plotted for a population of rFN neurons previously characterized using a comparable approach (Figure 6 C has been adapted from Figure 5 from Brooks and Cullen, 2009). (D) Average tuning curves computed by aligning the peak of each individual neuron's tuning curve. Average tuning curves are shown for bimodal and unimodal Purkinje cells (blue) for vestibular stimulation with the head oriented at different positions relative to the body. Again, for comparison, the average tuning curves of rFN neurons are superimposed (Figure 6 D has been adapted from Figure 6 from Brooks and Cullen, 2009).

Figure 7 - A simple linear population model of Purkinje cell integration can explain the responses of target bimodal neurons in deep cerebellar nuclei across all self-movement conditions. (A) Illustration of the convergence of multiple Purkinje cells onto a single neuron in the rostral fastigial nucleus (rFN), with different shades of red representing theoretical differences in the weighing of each Purkinje cell’s synapse with the target rFN neuron. (B) Schematic of the linear summation population model used to estimate the firing rate of a target neuron in the rFN. Each Purkinje cell’s weight was optimized to generate the best estimate of the average bimodal rFN neuron across conditions (Brooks and Cullen 2009). (C) Model performance as a function of the number of Purkinje cells. Black curve corresponds to model fit to the simple spike firing rates of all 73 Purkinje cells recorded during our three dynamic conditions (i.e., whole-body, body-under-head, and head-on-body movements. Blue curve corresponds to the model fit to simple spike firing rates of all 73 Purkinje cells during these same three dynamic conditions as well as simulated responses of these cells recorded in the gain-field condition (Fig. 6). The variability estimated from a population of rFN bimodal neurons previously described by Brooks and Cullen (2009) is represented by the green shaded band. Inset: the distribution of computed weights for each Purkinje cell modeled during our three dynamic conditions with 40 Purkinje cells, sorted based on average weight. (D) Estimated model firing rates based on a population of 40 Purkinje cells superimposed on the actual average firing rate of a bimodal rostral fastigial nucleus (rFN) neuron (grey shaded region). Solid black lines versus dashed blue lines illustrate firing rate estimations from models that included (i) the three dynamic head/body rotation conditions (left) versus (ii) the three dynamic conditions as well as the gain-field condition (right).
Supplementary figure captions

Figure 1 - figure supplement 1 - Purkinje cells show heterogeneity in their simple spike responses to vestibular stimulation. (A) The contribution of each kinematic term (i.e., position, velocity, acceleration) in estimating the firing rate for the preferred (left) and non-preferred (right) direction of whole-body movement, computed as the % drop in total variance accounted for (VAF) when removed from the full model. Neurons that did not significantly respond to the non-preferred direction are shown as grey bars. Note, we sorted Purkinje cells based on the importance of the velocity term, since this is what is predominately encoded by their target neurons in the rFN and vestibular nuclei. Interestingly, in the non-preferred direction, the acceleration term (yellow) contributes more to estimated firing rate (i.e., greater reduction VAF when removed) indicating that Purkinje cell responses generally led stimulation velocity. (B) The computed VAF (mean± 95% CI) in estimating the firing rate for the preferred (left) and non-preferred (right) direction of whole-body movement. Black and grey bars represent bimodal and unimodal Purkinje cells, respectively. The red area corresponds to non-significant VAF values computed from the same stimulation and shuffled inter-spike intervals (ISI). (C) The response of the Purkinje cells grouped as (i) linear, which demonstrated increased and decreased firing rate in the preferred and non-preferred directions, respectively, (ii) V-shape, which demonstrated increased firing rate in both directions, (iii) rectifying, that demonstrated increased firing rate in the preferred direction and minimal modulation in the non-preferred direction, and (iv) others that did not meet any of the mentioned criteria. (D) The pie chart illustrates the percentage of each category within the Purkinje cells.

Figure 2 - figure supplement 1 - Purkinje cells show heterogeneity in their simple spike responses to proprioceptive stimulation. (A) The contribution of each kinematic term (i.e., position, velocity, acceleration) in estimating the firing rate for the preferred (left) and non-preferred (right) direction of body movement (i.e., body-under-head) for bimodal Purkinje cells, computed as the % drop in total variance accounted for (VAF) when removed from the full model. Neurons that did not significantly respond to the non-preferred direction are shown as grey bars. Note, we sorted the Purkinje cells based on the importance of the velocity term, since this is what is predominately encoded by the target neurons in the rFN and vestibular nuclei. (B) The computed VAF (mean± 95% CI) in estimating the firing rate for preferred (left) and non-preferred (right) direction of whole-body movement. Black and grey bars represent bimodal and unimodal Purkinje cells, respectively. The red area corresponds to non-significant VAF values computed from the same stimulation and shuffled inter-spike intervals (ISI). (C) The response of the bimodal Purkinje cells, which are groups as (i) linear, which demonstrated increased and decreased firing rate in the preferred and non-preferred directions, respectively (ii) V-shape, which demonstrated increased firing rate in both directions, (iii) rectifying, that demonstrated increased firing rate in the preferred direction and minimal modulation in the non-preferred direction, and (iv) others that did not meet any of the mentioned criteria. (D) The pie chart illustrates the percentage of each category within the Purkinje cells.
Figure 2 - figure supplement 2 - Purkinje cells show heterogeneity in their simple spike responses to vestibular versus proprioceptive stimulation (A, B) Scatter plots comparing the sensitivity to vestibular and neck proprioceptive stimulation for unimodal (white circles) and bimodal (black circles) Purkinje cells for preferred (A) and non-preferred (B) direction of movement. The Grey shaded area corresponds to the Purkinje cells with larger sensitivity to vestibular compared to neck proprioceptive sensitivity. (C, D) Scatter plots comparing the phase of the responses to vestibular and neck proprioceptive stimulation for bimodal Purkinje cells for the preferred (C) and non-preferred (D) direction of movement. (E, F) The distribution of the neuronal sensitivity of the Purkinje cells simple spikes response to the vestibular stimulation for the preferred (E) and non-preferred (F) direction of movement. Open bars correspond to the cells that did not show a significant response to the neck proprioceptive stimulation (i.e., unimodal cells).

Figure 2 - figure supplement 3 – For most of the Purkinje cells, the responses to vestibular and neck proprioceptive stimulation were classified in different groups. (A) Venn diagram showing the number Purkinje cells that were grouped as linear, V-shape, rectifying, and other for vestibular and neck proprioceptive responses and their overlap (filled area). (B) The number of Purkinje cells that were classified in pairs of groups based on their response to vestibular (y-axis) and neck proprioceptive (x-axis) inputs.

Figure 3 - figure supplement 1 - Purkinje cell responses to combined vestibular–neck proprioceptive stimulation in the non-preferred direction of vestibular stimulation. (A, B) Polar plots illustrating the vestibular (blue) and neck proprioceptive (green) neuronal response sensitivities of Type I (A) and Type II (B) Purkinje cells for non-preferred direction of vestibular stimulation and complementary direction proprioceptive stimulation (i.e., body-under-head motion). Superimposed blue and green arrows represent the mean population vectors, respectively.

Figure 3 - figure supplement 2 – Polar representations of Purkinje cells simple spike response. Polar plots representing each individual Purkinje cells response ordered by increasing discrepancy between the summed and combined responses in the preferred direction. Response vectors predicted by the summation model (red) are superimposed on those for vestibular (blue), proprioceptive (green), and combined stimulation (black).

Figure 4 - figure supplement 1 – Purkinje cell simple spike responses to combined stimulation are well predicted by the linear summation of a given neuron’s responses to vestibular and proprioceptive stimulation when applied alone. (A, B) Comparison of estimated and predicted sensitivities (A) and phases (B) of Purkinje cell responses to head-on-body rotations in the non-preferred movement direction. The linear summation of a given neuron’s vestibular and neck proprioceptive sensitivities well predicted both measures in the combined condition. Blue lines and shading denote the mean ± 95% CI of linear fit.
Figure 5 - figure supplement 1 – Heterogeneity in Purkinje cell simple spike encoding of head and body movement for the non-preferred direction. (A) Scatter plot of the relationship between the head sensitivity ratio ($\frac{S_{\text{vest.+prop.}}}{S_{\text{vest.}}}$) and body sensitivity ratio ($\frac{S_{\text{prop.}}}{S_{\text{vest.}}}$) for the non-preferred direction. Histograms (top and right) illustrate the distributions of body and head sensitivity ratios, respectively. Orange versus red stars indicate ideal encoding of body versus head movement in space, respectively. For comparison, the red and orange shaded areas representing the distribution of values estimated for unimodal and bimodal rFN neurons (Brooks et al. 2009) are superimposed. (B) Distribution of coding indexes (see Methods). Positive and negative values correspond to agonistic and antagonistic responses to head vs. body encoding, respectively.

Figure 7 – figure supplement 1 – The distribution of the weights of the inputs to the model with 40 Purkinje cells projecting to a bimodal rFN neuron. The distribution of the Purkinje cell weights in a model with 40 Purkinje cells projecting to (A) Type I and (B) Type II bimodal rFN neuron that were classified as (A1, B1) linear vs. v-shaped vs. rectifying Purkinje cells, (A2, B2) bimodal vs. unimodal Purkinje cells, (A3, B3) Type I vs. Type II Purkinje cells, and (A4, B4) agonistic (i.e., same vestibular and proprioceptive sensitivity sign) vs. antagonistic (i.e., opposite vestibular and proprioceptive sensitivity sign).

Figure 7 – figure supplement 2 – The distribution of the weights of the inputs to a model with 40 Purkinje cells projecting to a unimodal rFN neuron. The distribution of the Purkinje cell weights in a model with 40 Purkinje cells projecting to (A) Type I and (B) Type II unimodal rFN neuron that were classified as (A1, B1) linear vs. v-shaped vs. rectifying Purkinje cells, (A2, B2) bimodal vs. unimodal Purkinje cells, (A3, B3) Type I vs. Type II Purkinje cells, and (A4, B4) agonistic (i.e., same vestibular and proprioceptive sensitivity sign) vs. antagonistic (i.e., opposite vestibular and proprioceptive sensitivity sign).

Figure 7 – figure supplement 3 – Modeling the mossy fiber inputs to unimodal fastigial neurons. (A) Schematic of a model with a mossy fiber input that is simulated as the summation of random patterns of responses to vestibular and neck proprioceptive input. The gains and phases were randomly drawn from a distribution comparable to that previously reported in the vestibular nuclei ($0.6\pm0.1$ (sp/s)/(deg/s) and $20\pm5$ deg, respectively; Mitchell et al. 2017). (B) The performance of the Purkinje cell population in predicting the response of the bimodal (top) and unimodal (bottom) rFN neurons in the presence (grey) and absents (red) of mossy fibers in (A).

Figure 7 – figure supplement 4 – Exploring the effect of systematically altering the distribution of gain and phase values in this simulated mossy fiber input. (A) Five different distributions of mossy fiber inputs. The reference distribution is similar to the neurons in the vestibular nuclei (red; gain: $0.6\pm0.1$ (sp/s)/(deg/s), phase: $20\pm5$ deg). Four other distributions were generated by systematically altering the distribution of gain and phase values for the reference distribution by i) doubling the gain (orange), ii) reducing the gain by half (dark blue),
iii) doubling the phase (blue), and iv) reducing the phase by half (green). (B) The performance of a population model of Purkinje cells projecting to a Bimodal Type I rFN neuron considering mossy fiber inputs with the five distributions shown in (A). The performance was similar for all distributions of mossy fibers. (C) The distribution of the weights of the Purkinje cells in the model with 40 Purkinje cells considering mossy fiber inputs with the distributions shown in (A). Changing the gain but not the phase of mossy fiber inputs affects the weighting of Purkinje cell inputs.

**Figure 7 – figure supplement 5 -** A simple linear population model of Purkinje cell integration can explain the responses of target unimodal neurons in deep cerebellar nuclei across all self-movement conditions. (A) Model performance as a function of the number of Purkinje cells. Black curves correspond to the population modeling that was performed on the simple spike firing rate of all 73 Purkinje cells recorded during three dynamic conditions (i.e., whole-body, body-under-head, and head-on-body movements). Blue curves correspond to the modeling of the simple spike firing rate of all 73 Purkinje cells during these same three dynamic conditions as well as the gain field condition (Fig. 5). The variability estimated from population of rFN unimodal neurons previously described by Brooks and Cullen (2009) is represented by the green shaded band. Inset: the distribution of computed weights for each Purkinje cell in a model with 40 Purkinje cells during our three dynamic conditions, sorted based on average weight. (B) Typical firing rate of unimodal neurons in the rostral fastigial nucleus (rFN) (grey shaded region) and the estimated firing rate based on a population of 50 Purkinje cells (mean ± SD) during three dynamic head/body rotation conditions (left) and the static changes in head-on-body position condition (right). We also performed population modeling on rFN type II cells and found similar results.
Figure 1

A

vestibular (whole-body)

Purkinje Cell 1 (linear)

head velocity

body velocity

simple spikes firing rate

trial #

Type II

resting discharge

Purkinje Cell 2 (v-shape)

Purkinje Cell 3 (rectifying)

head velocity (deg/s)

firing rate (sp/s)

firing rate (sp/s)

firing rate (sp/s)

100 deg/s

100 sp/s

100 sp/s

500 ms

B

preferred direction whole-body motion

Type II

Type I

vestibular sensitivity (sp/s)/(deg/s)

frequency (number of cells)

C

non-preferred whole-body motion

population average:

Type I

Type II
Figure 2

A

neck proprioceptive
(body-under-head)

stable
head

contra.

ipsi.

head
velocity

body
velocity

simple spikes
firing rate

trial #

B

preferred direction
body-under-head motion

C

non-preferred direction
body-under-head motion

neck proprioceptive sensitivity
(sp/s)/(deg/s)

frequency (number of cells)

population average:

unimodal

bimodal

Type I

Type II
Figure 3

(A) **Type I**

(B) **Type II**

(C) Vestibular & neck proprioceptive (head-on-body)

(D) Preferred direction

(E) Non-preferred direction
Figure 4

A  sensitivity (deg/s)/(sp/s)

B  phase (deg)

R² = 0.77

R² = 0.75

bimodal
unimodal
best fit
unity line
Figure 5

A

- Bimodal rFN
- Unimodal rFN

- Whole-body
- Body-under-head
- Head-on-body

B

- % rFN cells
- % Purkinje cells

- Agonistic coding index
- Antagonistic coding index

- Head (unimodal)
- Body (bimodal)
- Body-dominant (bimodal)
- Head-dominant (bimodal)
- Head and body (bimodal)

Purkinje cell: rFN:
- Bimodal
- Unimodal

Body-centered
Head-centered
Figure 6

A

- bimodal Purkinje cell
- unimodal Purkinje cell

Head velocity

Firing rate

Sensitivity vs. head-on-body position (deg)

B

- bimodal Purkinje cell
- unimodal Purkinje cell

Change in sensitivity vs. head-on-body position (deg)

C

- % of Purkinje cells
- % of rFN cells

D

- Change in sensitivity vs. head-on-body position (deg)
Figure 7

A. Anterior vermis with Purkinje cells and rFN cell.

B. Purkinje cells under dynamic head/body rotation conditions:
   - Whole-body
   - Body-under-head
   - Head-on-body

C. Goodness of fit (R²) for rFN cell population estimation:
   - Without gain-field condition
   - With gain-field condition

D. Dynamic head/body rotation conditions:
   - Whole-body
   - Body-under-head
   - Head-on-body

Static changes in head-on-body position (gain-field condition):
   - -30°
   - -15°
   - 0°
   - +15°
   - +30°

Population model estimation:
   - Without gain-field condition
   - With gain-field condition
Figure 1 - figure supplement 1

A

preferred direction

vestibular sensitivity

% drop in VAF (normalized)

B

non-preferred direction

vestibular sensitivity

velocity term
acceleration term
position term

C

vestibular sensitivity (sp/s)/(deg/s)
contralateral head-on-body direction

linear
rectifying
v-shape
others

D

15% linear
33% rectifying
33% others
19% v-shape

unimodal
bimodal

shuffled data
Figure 2 - figure supplement 2

A

Preferred direction

B

Non-preferred direction

C

D

E

Preferred direction

Whole-body motion

F

Non-preferred direction

Whole-body motion
A

Figure 2 - figure supplement 3

B

Change in Purkinje cells type

response to vestibular stimuli

<table>
<thead>
<tr>
<th></th>
<th>linear</th>
<th>rectifying</th>
<th>v-shape</th>
<th>others</th>
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<td>2</td>
<td>3</td>
<td>8</td>
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<tr>
<td>others</td>
<td>2</td>
<td>9</td>
<td>4</td>
<td>9</td>
</tr>
</tbody>
</table>

response to neck proprioceptive stimuli
Figure 3 - figure supplement 1

A

Type I

B

Type II

individual cell:

vest.

neck prop.

population average:

vest.

neck prop.
Figure 4 - figure supplement 1

A

sensitivity (deg/s)/(sp/s)

R² = 0.66

estimation, head-on-body

B

phase (deg)

R² = 0.82

estimation, head-on-body
Figure 5 - figure supplement 1

A

[Graph showing the relationship between the sensitivity ratio for body and head.

B

[Bar graph showing the percentage of Purkinje cells with different sensitivities.

Purkinje cell:
- rFN:
- body sensitivity ratio
- head sensitivity ratio

Body sensitivity ratio
- head (unimodal)
- body (bimodal)
- body-dominant (bimodal)
- head-dominant (bimodal)
- head and body (bimodal)

Graph legend:
- bimodal
- unimodal
- body-centered
- head-centered
Figure 7 - figure supplement 2

Unimodal Type I

A1

Unimodal Type II

B1

A2

P cells weight
probability
Purkinje cell

B2

P cells weight
probability
Purkinje cell

A3

P cells weight
probability
Purkinje cell

B3

P cells weight
probability
Purkinje cell

A4

P cells weight
probability
Purkinje cell

B4

P cells weight
probability
Purkinje cell
Figure 7 - figure supplement 3

A

Bimodal Type I

Bimodal Type II

Unimodal Type I

Unimodal Type II

Modeling performance ($R^2$) vs. Number of Purkinje cells

- Bimodal Type I: model performance estimated from single rFN
- Bimodal Type II: model performance for Purkinje cells and simulated mossy fibers
- Unimodal Type I: model performance for Purkinje cells
- Unimodal Type II: model performance for Purkinje cells and simulated mossy fibers

Gain & phase vestibular nuclei

Vestibular nuclei

Neck proprioceptive stimulation

Whole-body stimulation

Simulated mossy fibers

Purkinje cells

rFN
Figure 7 - figure supplement 4

A

Modeling performance ($R^2$) gain and phase similar to VN

Number of Purkinje cells with mossy fiber input:

- 0.5
- 1.0

B

Probability

P cells weight

C

Probability

P cells weight

- estimated from single rFN
- gain and phase similar to VN
- x2 gain, same phase
- x0.5 gain, same phase
- same gain, x2 phase
- same gain, x0.5 phase

- gain and phase similar to VN
- x2 gain, same phase
- x0.5 gain, same phase
A. unimodal rFN

- Figure 7 - figure supplement 5

- Purkinje cells

- goodness of fit ($R^2$)

- head velocity

- body velocity

- rFN firing rate

- population model estimation:
  - without gain-field condition
  - with gain-field condition

B. dynamic head/body rotation conditions

- whole-body
- body-under-head
- head-on-body

- static changes in head-on-body position (gain-field condition)

- -30° -15° 0° +15° +30°