

Stimulus-Independent Attentional Modulation in Cerebellar Visual Regions

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Spatial attention shapes neural activity across multiple cortical regions, and recent studies have demonstrated spatially selective attentional signals in cerebellar visual regions. However, it remains unclear whether these signals extend across the broader network of cerebellar visual representations and whether they share key functional properties of attentional modulation observed in cortical visual areas. Using fMRI, we measured brain activity in 50 participants (30 females) as they performed a covert spatial attention task in which attention was directed to the left or right visual hemifield, followed by visual stimuli of varying contrast or no stimulus. We showed that distributed activity patterns in the cerebellum reliably distinguished the attended hemifield, replicating previous findings of spatially selective attentional signals in Lobules VIIb/VIIIa and extending these findings to Lobule VI and Lobules VIIIb/IX/X. These regions largely overlapped with topographically organized cerebellar visual maps, indicating that attentional modulation operates within representations of visual space. Critically, attentional modulation was observed even in the absence of postcue stimulus presentation and was invariant across stimulus contrast, consistent with additive attentional effects previously described in cortical visual areas. We further identified nonspatial, stimulus-independent cerebellar attentional signals, suggesting contributions to attentional control beyond spatial selection. Finally, comparisons with motion-evoked responses revealed systematic differences across cerebellar visual regions in the relative contribution of attentional and sensory signals. Together, these findings demonstrate that spatially selective attention is represented across multiple cerebellar visual maps and shares functional properties with attentional modulation in cortical visual areas while revealing functional heterogeneity within the cerebellum.

Key words: cerebellum; fMRI; visual attention; visual cortex

Significance Statement

Previous work demonstrated spatially selective attentional signals in cerebellar Lobules VIIb/VIIIa, but it remains unclear whether these signals extend across the broader network of cerebellar visual representations or share key functional properties of attentional modulation observed in cortical visual areas. Here, we show that multiple cerebellar visual representations contain spatially selective attentional signals that are independent of postcue stimulus presence and invariant across stimulus contrasts, paralleling attentional modulation in cortical visual areas. We also identify nonspatial stimulus-independent attentional signals and reveal regional differences in the relative contribution of attentional and sensory signals in the cerebellum. These findings establish the cerebellum as an active and functionally heterogeneous component of spatial attention.

Introduction

Beyond its established role in motor control, the human cerebellum is increasingly recognized as contributing to cognitive functions, including visuospatial attention. Early work demonstrated that cerebellar activity is modulated during visual selective attention tasks and functionally dissociable from motor responses,

suggesting a role beyond motor execution (Allen et al., 1997). Connectivity-based studies further indicated that cerebellar activity is coordinated with neocortical attention networks, including interactions with dorsal attention regions and motion-sensitive area V5/MT (Kellermann et al., 2012; Brissenden et al., 2016). More recently, multivariate analyses have revealed that the locus of covert spatial attention could be decoded from cerebellar activity patterns, with cerebellar Lobules VIIb/VIIIa exhibiting an ipsilateral bias consistent with corticocerebellar anatomical connections (Brissenden et al., 2018). Together, these findings establish that the cerebellum participates in spatial attention and can contain spatially specific information.

However, the functional characteristics of cerebellar attentional signals and how they relate to well-established properties of attention in cortical visual systems remain poorly understood.

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In the cortex, attention is known to reshape neural representations across multiple levels of visual processing, from retinotopically organized visual representations to higher-order semantic representations (Brefczynski and DeYoe, 1999; Çukur et al., 2013). Attention modulates activity in retinotopically organized early visual areas in a spatially specific manner, producing stimulus-independent and contrast-invariant (additive) increases in BOLD responses (Buracas and Boynton, 2007; Li et al., 2008; Murray, 2008; Sylvester et al., 2009). Whether cerebellar attentional signals share these defining properties or instead depend on sensory input is unknown.

Another key unresolved issue is the relationship between attentional modulation and topographically organized cerebellar visual representations. While prior work has identified spatially specific attentional coding in Lobules VIIb/VIIIa (Brissenden et al., 2018), more recent high-resolution mapping studies have revealed additional cerebellar visual field representations, including in Lobule VIIIb and the oculomotor vermis (OMV; van Es et al., 2019). It remains unclear whether attentional modulation aligns with these broader topographic maps or is restricted to a subset of cerebellar regions.

Here, we addressed these questions by measuring cerebellar activity using fMRI while participants performed an endogenous covert visuospatial attention task. Unlike overt visuospatial attention, in which gaze is directed toward the attended location, covert attention involves allocating attention while maintaining fixation. This distinction is particularly important when studying cognitive functions in the cerebellum, because it minimizes the confounding influence of eye movements, allowing attentional signals to be distinguished from the cerebellum's well-established role in oculomotor control. In this study, participants were instructed to allocate attention to the left or right visual hemifield while maintaining central fixation, after which stimuli of varying contrast or no stimulus were presented. This design allowed us to dissociate attentional deployment, specifically the voluntary allocation of attention toward a cued spatial location prior to the appearance of the target stimulus, from sensory responses and to directly test whether cerebellar attentional modulation is spatially selective, stimulus-independent, and contrast-invariant.

We first used multivoxel pattern analysis (MVPA) to assess whether cerebellar activity contains spatially selective attentional information. This analysis allowed us to replicate prior evidence that the locus of covert spatial attention can be decoded from cerebellar activity patterns and to determine whether such information extends beyond previously identified Lobules VIIb/VIIIa to additional topographically organized cerebellar visual areas. We then used univariate analyses to isolate attentional modulation in the absence of postcue stimulus presentation and to characterize how attentional effects interact with stimulus contrast. Finally, we compared attentional and sensory responses to assess the relative contribution of these signals across cerebellar regions. Together, these analyses provide a comprehensive characterization of cerebellar attentional modulation and determine whether spatial attention modulates cerebellar activity in a manner similar to cortical visual areas.

Materials and Methods

Participants

Fifty adults (30 females; mean age, 24.35 years; SD = 3.57 years) participated in the study. Participants were recruited through university advertisements and online postings. All participants were between 18 and 30 years old at the time of enrollment, reported normal or corrected-to-normal vision (via contact lenses or glasses), and had no

history of epilepsy or other neurological disorders. Participants were also screened to ensure they were not taking medications known to affect cognitive or visual processing. Prior to participation, all participants provided written informed consent. Participants received financial compensation for their time. The study was approved by the Institutional Review Board at the University of Washington.

Experimental design

Stimuli were generated and presented using MATLAB and the Psychtoolbox-3 software extensions. Stimuli were displayed on a BOLDscreen 32 LCD monitor (Cambridge Research Systems) against a mean-luminance gray background, at a screen resolution of 1,920 × 1,080 pixels and a refresh rate of 60 Hz. Participants viewed stimuli binocularly from a fixed distance of 120 cm.

Attention task. Each trial consisted of three periods: an attention-cue period (700 ms), a stimulus presentation period (300 ms), and a response period (2,000 ms). Participants maintained fixation on a central horizontal fixation bar (length, 0.55°) throughout the experiment. During the cue period, a subtle triangular marker (base length, 0.1°; contrast, 10%) appeared at one randomly selected end of the fixation bar, forming an arrow that indicated the part of the visual field to attend. Subsequently, two circular Gabor gratings (orientation, 0°; diameter, 2°) appeared bilaterally, positioned at 3° eccentricity from fixation, with a spatial frequency of 1 cycle per degree. A Gaussian envelope (SD = 0.4°) was applied to taper stimulus edges. The two gratings drifted to either left or right randomly and independently, with a temporal frequency of 4 Hz, animated through 36 phase steps to produce smooth motion. During the response period, participants indicated the perceived motion direction of the attended grating via a two-button response box (left button for leftward, right button for rightward; Current Designs) with their right hand. Stimuli appeared at three contrast levels: 0% (no stimulus presented after the cue), 6%, and 50%. Participants did not respond during 0% contrast trials. There were six experimental conditions (2 cue directions × 3 contrasts). This design dissociated attentional deployment from sensory input and allowed independent manipulation of stimulus contrast.

Every experiment run comprised 16 trials per condition and 32 no-event fixation trials, totaling 128 trials per run. Each run lasted 396 s, consisting of 128 trials (3 s per trial) followed by 12 s of fixation after the final trial. Participants completed four runs of the experiment, with trial order randomized according to an eighth-order m-sequence optimized for efficient estimation of hemodynamic responses (Buracas and Boynton, 2002). Prior to MRI scanning, participants completed a behavioral training session and received feedback on their performance to ensure task proficiency. During MRI scanning, the mean response accuracy for trials involving motion-direction discrimination (6 and 50% contrast trials) was 90.73% (SD = 12.87%, $N = 50$). Using a linear mixed-effects (LME) model predicting accuracy from run number (treated as a categorical variable), with subject modeled as a random effect, we found a significant effect of run number on accuracy ($F_{(3,147)} = 2.89$, $p = 0.038$). Post hoc pairwise comparisons revealed that this effect was driven by higher accuracy in the first run than in the last run (Δ accuracy = 3.25%, $p = 0.033$, Tukey-adjusted). No other pairwise comparisons were significant. This pattern suggests a modest decline in performance over the course of the experiment, potentially reflecting fatigue. Following instructions, participants made no button-press response during no-event trials (mean accuracy = 99.73%, SD = 0.58%, $N = 50$) and 0% contrast trials (mean accuracy = 99.70%, SD = 0.56%, $N = 50$).

Primary visual cortex (V1) localizer. The V1 localizer used two types of circular black-and-white checkerboard stimuli: a central checkerboard at fixation and bilateral peripheral checkerboards (all had diameter, 2°; with individual squares measuring 0.5°). Peripheral checkerboards were presented bilaterally at 3° eccentricity from fixation, matching the position of stimuli in the attention task. Checkerboards flickered at 8 Hz, alternating between two contrast-reversed configurations. The localizer followed a block design consisting of alternating central and

peripheral stimulus blocks, each lasting 10 s, totaling 20 blocks. Throughout the experiment, participants maintained fixation at a central bullseye fixation cue.

Middle temporal area (MT+) localizer. The MT+ localizer (hereafter also referred to as the motion localizer) used a block design comprising alternating stimulus and rest blocks. During every trial within a stimulus block, two circular drifting gratings (diameter, 2°) appeared bilaterally at 3° eccentricity, with a spatial frequency of 1 cycle per degree, a temporal frequency of 4 Hz, and a 16% contrast. Gratings animated through 36 phase increments to produce drifting motion. The orientations of left and right gratings were independently and randomly selected from eight possibilities (0, 45, 90, 135, 180, 225, 270, and 315°). Each stimulus block consisted of 20 trials and lasted for 10 s, followed by a 10 s rest block displaying only the bullseye fixation cue. A total of 10 stimulus blocks were presented, each paired with a rest block.

MRI acquisition and preprocessing

MRI data were acquired on a Siemens Prisma 3 Tesla MRI scanner with a 64-channel head coil at the Center for Human Neuroscience at the University of Washington in Seattle, Washington. T1-weighted MPRAGE structural images were obtained (sagittal; TR, 2,530 ms; TE, 1.69 ms; flip angle, 7°; 1 mm isotropic voxel resolution; FOV, 176 × 256 × 256 mm). Functional images were collected using a multiband gradient-echo echo-planar sequence (TR, 1,000 ms; TE, 30 ms; flip angle, 64°; 3 mm isotropic voxel resolution; FOV, 156 × 222 × 222 mm; multiband factor, 4). Fifty-two axial slices were acquired without gaps, covering the whole brain. Each participant completed four attention-task scans and two localizer scans within a single scanning session.

Functional MRI data were preprocessed using the *fMRIPrep* (version 23.0.1 & 23.0.2) pipeline. Preprocessing steps included head-motion estimation, fieldmap-based susceptibility distortion correction, coregistration of functional data to each participant's anatomical reference image, and resampling to the standard *MNI152NLin2009cAsym* space. Functional images were denoised using the MATLAB fMRI Denoising Toolbox (Mascali et al., 2021). The denoising model included the discrete cosine basis regressors generated by *fMRIPrep* to account for low-frequency signal drifts, together with first-order polynomial detrending. The residual time series were written out with the original mean signal restored and were then used for subsequent analyses.

Eye tracking

Eye tracking was performed in all tasks using an EyeLink 1000 system (SR Research) sampling at 1,000 Hz. Participants were instructed to maintain central fixation throughout the attention and localizer scans. Post hoc drift correction was applied to mitigate potential calibration errors. Specifically, during each 10 s epoch, eye-position coordinates were re-centered by subtracting the offset between the mean fixation position and the expected fixation location (center of the screen). Eye-tracking data were available for 44 participants during the attention task and V1 localizer and 43 participants during the motion localizer. Data from the other participants were excluded because the recordings contained predominantly invalid samples and therefore did not permit reliable estimation of gaze position or eye movements.

To assess fixation behavior and potential eye-movement confounds during the attention task, we quantified several measures from the eye-tracking data. Fixation compliance during the attention task and localizers was assessed using the proportion of total fixation time during which drift-corrected gaze position remained within 1° of visual angle from the center of the screen. To characterize whether eye-movement behavior during the attention task was dependent on stimulus contrast, we quantified the total number of saccades and the total saccade amplitude within each trial. The total number of saccades reflects the frequency of eye movements, whereas total saccade amplitude reflects the cumulative magnitude of eye displacement. Trials may differ in the number of saccades despite having similar cumulative displacement or vice versa. We therefore analyzed both measures separately to characterize distinct sources of eye-movement variability. To assess whether cue direction systematically biased eye movements toward the attended location,

saccades were classified according to the angle of the movement vector, with angles between −45 and 45° classified as rightward and angles between 135 and 180° or between −180 and −135° classified as leftward. A directional bias index was computed by subtracting leftward eye-movement measures from rightward eye-movement measures.

To evaluate the potential influence of eye movements on the fMRI results, first-level GLMs were re-estimated with nuisance regressors derived from the eye-tracking data. Regressors included the average horizontal and vertical eye positions, together with HRF-convolved regressors describing total saccade amplitude and the numbers of leftward and rightward saccades per TR. Task-related beta estimates from the original and eye-movement-corrected GLMs were compared with assess the influence of eye movements on the estimated neural responses. In addition, beta estimates associated with the leftward- and rightward-saccade regressors were analyzed to determine whether directional saccades produced hemisphere-dependent activation patterns that could account for the observed spatially selective attentional effects.

Data analysis

Cerebellar isolation, normalization, and flatmap visualization. The cerebellum was isolated from each participant's T1-weighted anatomical image using the SUIT toolbox (version 3.7; Diedrichsen, 2006) implemented in MATLAB 2025b (MathWorks) with SPM (version 25.01.02). The isolation procedure generated a cerebellar mask and segmented gray and white matter within the isolated volume. Manual inspections were performed to ensure accurate delineation of cerebellar boundaries. The isolated cerebellum was then nonlinearly normalized to the SUIT template, and functional maps were resliced into SUIT space for group-level analyses. In cases where participant-specific region of interest (ROI) extraction was performed in native space, atlas-derived ROIs were transformed from SUIT space back into each participant's native anatomical space using SUIT reslicing procedures. Cerebellar maps were visualized using SUITPy (version 2.0.0) in Python (version 3.12.2), which provides a flatmap representation of the cerebellum (Diedrichsen and Zotow, 2015). The flatmap is not a true surface reconstruction but a voxel-based projection of volumetric data onto a two-dimensional representation of the cerebellar cortex, involving sampling and summarizing across multiple voxels. For display purposes, flatmap values were defined as the minimum or maximum value across sampled voxels. Because this approach emphasizes extreme values, it may bias the apparent spatial extent or magnitude of effects.

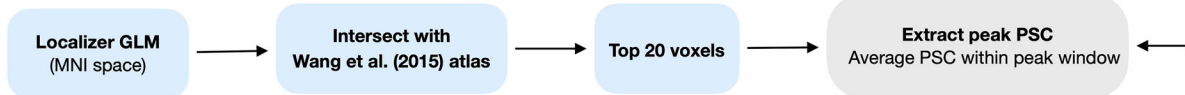
MVPA and feature weight mapping. MVPA was conducted to determine whether spatial attention directed to the left versus right visual hemifield could be decoded from cerebellar activation patterns. The analysis pipeline was adapted from prior work (Brissenden et al., 2018). The overall MVPA workflow is illustrated in Figure 1B.

For each participant, trial-wise activation patterns were first extracted in native space and then transformed to SUIT space. Only trials corresponding to left- and right-cue conditions were included in the analysis, whereas no-event trials were used for baseline normalization. Voxel time series were converted to percent signal change (PSC) relative to the mean signal of no-event trials within each run. This normalization was performed separately for each run to reduce run-wise baseline differences. Voxel features were defined as the mean PSC of 4–6 s after each trial onset.

Classification was performed using a linear support vector machine (SVM; LinearSVC, scikit-learn, version 1.8.0; Python, version 3.12.2) with leave-one-run-out cross-validation. In each fold, one run was held out for testing while the remaining three runs were used for training. Within each training fold, voxel features were standardized to z-scores using the mean and standard deviation estimated from the training data. The same transformation was then applied to the held-out test data to ensure that training and test data were represented in the same feature space. Principal component analysis (PCA) was then applied to the standardized trial-by-voxel feature matrix to reduce the dimensionality of the voxel feature space. The number of principal components was set to $N_{\text{trials}} - 1$ (N_{trials} number of training samples in that fold). Test data were projected onto the principal axes derived from the training data.

A. ROI definition and PSC extraction

Cortical ROIs (V1, MT+)



Cerebellar ROIs



B. MVPA analysis pipeline

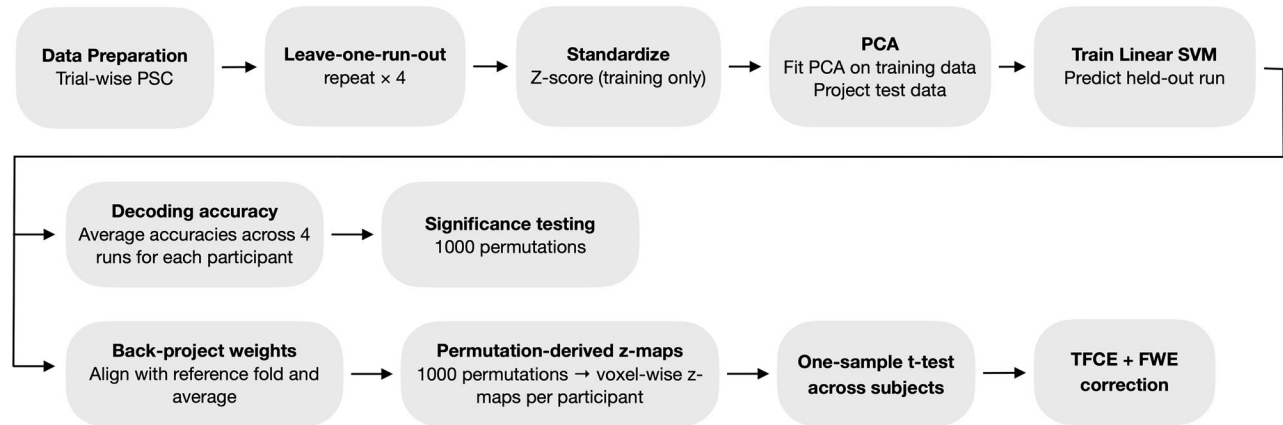


Figure 1. Overview of the ROI definition, PSC extraction, and MVPA analysis pipelines. **A**, Cortical and cerebellar ROI definition and PSC extraction workflows. Cortical ROIs were defined from independent functional localizers, whereas cerebellar ROIs were defined from the attention-task GLM or the MVPA feature weight maps. ROIs were then used to extract peak PSC values. **B**, Overview of the MVPA pipeline used to decode the attended visual hemifield from cerebellar activation patterns. Trial-wise PSC patterns were used for leave-one-run-out cross-validation, feature standardization, PCA, and linear SVM classification. Decoding accuracy and feature weight maps were evaluated at the group level using permutation testing.

The regularization parameter of the linear SVM was optimized using nested leave-one-run-out cross-validation within the training set. Classification accuracy was computed on the held-out test run and averaged across folds to obtain a subject-level decoding accuracy.

To characterize the spatial distribution of information contributing to decoding, voxelwise weight maps were reconstructed for each cross-validation fold. For each fold, the weight vector learned in principal component space was back-projected into voxel space. Due to the sign indeterminacy inherent in PCA, weight maps from different folds can exhibit global sign inversions despite representing equivalent decision boundaries. To ensure consistent orientation prior to averaging, fold-wise weight maps were aligned by correlating each map with a reference fold and multiplying the map by -1 when the correlation was negative. The aligned weight maps were then averaged across folds to obtain a stable subject-level weight map. Left- and right-cue trials were coded such that positive weights indicated greater evidence for right-cue trials, whereas negative weights indicated greater evidence for left-cue trials.

Statistical significance of decoding accuracy was assessed using permutation testing with 1,000 shuffles of labels, in which class labels (left- vs right-cue) were randomly permuted within runs. A group-level decoding accuracy was computed by averaging accuracies across all participants. The p value was defined as the proportion of permuted group accuracies greater than or equal to the observed group accuracy.

To evaluate the statistical significance of voxelwise feature weights, a null distribution of weights was generated using the same permutation procedure. For each voxel and subject, the proportion of permuted weights that were as or more extreme than the observed weight was computed and converted to z -scores while retaining the original sign of the weights. These subject-level z -maps were then entered into a group-level analysis. For each voxel, a one-sample t test was performed to assess

whether weight-related z -scores across subjects differed significantly from zero. Prior to computing voxelwise t statistics, the across-subject variance was spatially smoothed using a 4 mm full-width at half-maximum Gaussian kernel. Threshold-free cluster enhancement (TFCE) was then applied to the t statistic maps to enhance cluster-like structure without requiring an arbitrary cluster-forming threshold (Smith and Nichols, 2009). To correct for familywise error, a null distribution of TFCE scores was constructed by selecting the maximum TFCE value across all voxels for each permutation. Voxelwise p values were computed as the proportion of permutation-derived TFCE maxima that were as or more extreme than the observed TFCE score at each voxel.

Analyses using general linear model. General linear model (GLM) analyses were conducted using the Nilearn Python library (version 0.11.1; Python, version 3.12.2). First-level GLMs were fitted using task regressors convolved with the SPM canonical hemodynamic response function, along with temporal derivatives and a constant term. For the attention task, GLMs included 13 regressors: one regressor and its temporal derivative for each of the six task conditions, plus a constant term. No-event (fixation) periods were not modeled explicitly and therefore served as an implicit baseline. For the V1 localizer, GLMs included three regressors: one regressor and its temporal derivative modeling peripheral stimulus blocks, plus a constant term, with central stimulus blocks left unmodeled and serving as an implicit baseline. For the motion localizer, GLMs were similarly specified with three regressors: one regressor and its temporal derivative modeling stimulus blocks, plus a constant term, with rest blocks left unmodeled and serving as an implicit baseline.

GLMs were estimated in task-appropriate reference spaces. For the attention task, first-level GLMs were fitted in each participant's native

space to preserve individual cerebellar anatomy. Resulting contrast maps were subsequently resliced into SUIT space using the SUIT normalization pipeline, where second-level random-effect analyses were conducted. For the localizer scans used to define V1 and MT+, GLMs were estimated in Montreal Neurological Institute (MNI) space to enable intersection with probabilistic atlases defined in MNI space.

Localization of cerebellar ROIs. The overall workflow for ROI definition and PSC extraction is summarized in Figure 1A. ROI definition and subsequent analyses were performed on independent contrasts or conditions where possible. ROIs within the cerebellum were defined using contrasts from the attention-task GLM described above. The contrast of interest compared the average of left- and right-cue-only (0% contrast) conditions against an implicit baseline modeled using no-event trials, identifying regions engaged during attentional orienting independent of postcue stimulus.

The resulting group-level statistical map was thresholded at $p < 0.05$ (two-sided, uncorrected) and subsequently smoothed with a 4 mm FWHM Gaussian kernel to improve spatial contiguity. Significant clusters were labeled as medial Lobule VI, lateral Lobule VI, medial Crus II/Lobule VIIb, or lateral Lobule VIIb based on the cerebellar anatomical atlas described by [Diedrichsen et al. \(2009\)](#). Medial–lateral divisions were defined by cutoffs at $x = -19$ mm (left hemisphere) and $x = 19$ mm (right hemisphere) in SUIT space.

Because Lobules VIIIb/IX/X were not reliably identified by the cue-only contrast, ROIs in these regions were instead defined based on significant clusters derived from the MVPA. As a result, these ROIs were not independent of the multivariate analysis used to assess spatial selectivity.

These ROIs defined using group statistics were then resliced back into each participant's native space. Within each ROI, the 10 voxels showing the highest z -scores for the cue-only versus baseline contrast were selected for PSC extraction. After reslicing the group-defined ROIs into each participant's native space, the mean ROI sizes across participants and hemispheres were 14 voxels for medial Lobule VI, 58 voxels for lateral Lobule VI, 26 voxels for medial Crus II/Lobule VIIb, and 14 voxels for lateral Lobule VIIb. Given the relatively small size of some cerebellar ROIs, 10 voxels were selected as a practical threshold that could be applied consistently across most ROIs. In some cases, fewer than 10 voxels were identified within the target ROI. This occurred for one participant in the left medial Lobule VI (7 voxels), one participant in the left lateral Lobule VIIb (9 voxels), seven participants in the right medial Lobule VI (mean = 7.9 voxels), and eight participants in the right lateral Lobule VIIb (mean, 7.5 voxels). Time courses of the selected voxels during the attention task were then extracted. Each trial's time course spanned 17 s, starting 2 s before trial onset. PSC was computed using the average signal from no-event trials as the baseline, such that $PSC = \frac{\text{signal} - \text{baseline}}{\text{baseline}} \times 100$. Time courses were then averaged across all trials within the same condition.

Localization of cerebral cortical areas V1 and MT+. First-level GLMs for the localizer scans were fitted in MNI space using the Nilearn framework described above. Task-specific regressors (V1, peripheral vs central checkerboard; MT+, stimulus present vs absent) were included in the design matrix. The resulting statistical maps were then intersected with a probabilistic visual topography atlas ([Wang et al., 2015](#)). To account for individual variability in visual cortex anatomy, atlas-defined V1 and MT+ regions were thresholded at 10% probability. V1 was defined by combining dorsal and ventral components (V1d and V1v), while MT+ was defined by merging TO1 and TO2. To maintain a consistent ROI size across participants, the 20 most responsive voxels were selected from each cortical ROI, following [Kolodny et al. \(2020\)](#). Time courses of the selected voxels were extracted and corrected the same way as the cerebellar ROIs.

Analysis using LME models. All statistical analyses were conducted in R (version 4.3.1). LME models were implemented using the *lme4* package, and statistical inference was performed using the *lmerTest* package. Fixed effects were evaluated using Type III F tests with Satterthwaite's

approximation for degrees of freedom. Post hoc pairwise comparisons were conducted using the *emmeans* package, with p values adjusted for multiple comparisons.

For each ROI, peak PSC during experimental trials was analyzed using a separate LME model. Peak PSC was defined as the mean BOLD response within a predefined poststimulus time window. In cerebral cortical areas (V1 and MT+), peak PSC was calculated by averaging PSC values from 4 to 5 s after trial onset. In cerebellar regions, peak PSC was calculated by averaging PSC values from 4 to 6 s after trial onset. These time windows were selected based on visual inspection of group-averaged trial-locked BOLD time courses spanning 2 s before and 14 s after trial onset (Fig. S1). Cortical regions exhibited peak responses between 4 and 5 s, whereas cerebellar regions showed slightly delayed peaks between 4 and 6 s after trial onset. Analysis windows were centered on the observed peak responses to capture the maximal response amplitude. Peak PSC values were then averaged across trials, yielding one value per subject, condition, and ROI.

For each ROI, the LME model included three categorical fixed effects: cue direction (left, right), hemisphere of the ROI (left, right), and stimulus contrast (cue-only, low-contrast, high-contrast), along with all two-way and three-way interactions. Subject was included as a random effect to account for repeated measurements within individuals. The model was specified as $PSC \sim \text{cue direction} \times \text{hemisphere} \times \text{contrast} + (1 | \text{subject})$.

Results

We tested whether covert spatial attention modulates activity in cerebellar visual regions and whether such modulation exhibits properties characteristic of cortical visual areas. Participants performed a motion-direction discrimination task in which attention was directed to the left or right visual hemifield, followed by stimuli of varying contrast (6 or 50%) or no stimulus (0% contrast; Fig. 2). This design allowed us to dissociate attentional deployment from postcue sensory input and to assess whether cerebellar responses are spatially selective, stimulus-independent, and contrast-invariant.

Ipsilateral attentional coding in topographically organized cerebellar regions

We first asked whether cerebellar activity represents the spatial locus of attention. Given prior evidence for ipsilateral representation of the visual field in the cerebellum ([Brissenden et al., 2018](#); [van Es et al., 2019](#)), we hypothesized that topographically organized cerebellar visual regions would exhibit spatially selective activity patterns; specifically, left- and right-cue trials would evoke distinct patterns of activity in the cerebellum.

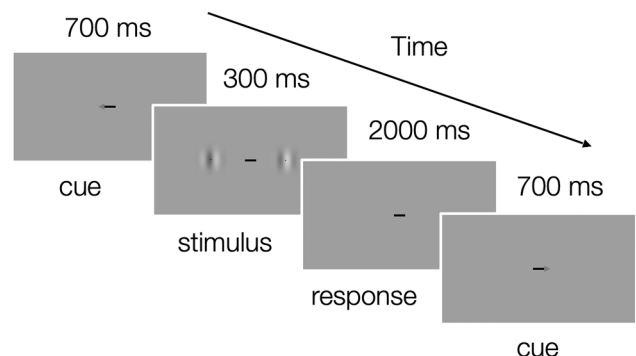


Figure 2. Experimental paradigm. Each trial consisted of an attention-cue period (700 ms), a stimulus presentation period (300 ms), and a response period (2,000 ms). Participants maintained fixation at a central fixation bar throughout the experiment. During the attention-cue period, participants were directed to covertly attend to the left or right visual hemifield following a cue. Two drifting Gabor gratings were then presented bilaterally, and participants reported the direction in which the attended grating drifted.

To test this hypothesis, we conducted an MVPA using a linear SVM to decode allocation of attention to the left versus right visual hemifield. Our analysis closely followed the pipeline described by Brissenden et al. (2018). Features were restricted to voxels within the cerebellar cortex, and trials were pooled across all stimulus contrast levels. Mean classification accuracy was 55.74% (SEM, 0.62%), which was significantly above chance based on permutation testing ($p = 0.027$). This result indicates that cerebellar activity contains information about the attended visual hemifield.

To determine which regions contributed to classification performance, we examined voxelwise classifier feature weights derived from the SVM. These weights quantify the contribution of individual voxels to distinguishing left- from right-cue trials (Fig. 3). Because postcue visual stimuli were presented in both hemifields regardless of cue direction, classification could not rely solely on sensory-driven responses. Instead, the feature weights reflect attentional modulation beyond baseline visual stimulation. Statistical significance of feature weights was assessed with a null distribution generated from 1,000 permutations, and TFCE was applied to identify clusters that reliably contributed to classifier decisions.

Previous work has shown that attentional modulation in cerebellar Lobules VIIb/VIIIa is spatially selective and exhibits ipsilateral coding of attended hemifields (Brissenden et al., 2018). Here, we replicated this effect by identifying clusters in medial Crus II, Lobule VIIb, and Lobule VIIIa that reliably contributed to classification of the attended hemifield (Fig. 3A,B). Specifically, a cluster in the left cerebellum biased classification toward left-cue trials, whereas a cluster in the right cerebellum

biased classification toward right-cue trials. In addition, we identified significant clusters in medial Lobule VI (Fig. 3A,B) and Lobules VIIIb/IX/X (Fig. 3A,C) that showed the same ipsilateral attentional coding. Notably, regions that demonstrated spatially selective attentional coding largely overlapped with cerebellar regions that were found to contain topographic representations of visual space (van Es et al., 2019; Fig. 3A, white contour).

Visual attention engages the cerebellum in the absence of postcue stimulus presentation

We next asked whether cerebellar activity is modulated by attention in the absence of postcue stimulus presentation, which would indicate engagement of top-down attentional processes independent of sensory input. To address this, we analyzed trials in which no stimulus followed the attention cue ("cue-only" trials), thereby isolating attentional deployment from postcue stimulus-evoked responses.

A GLM contrasting cue-only trials (left and right cues combined) with baseline (no-event trials) revealed significant activation in medial Lobule VI, Crus II, and Lobule VIIb, demonstrating that these regions, previously shown to represent the spatial locus of attention, are engaged by attention even in the absence of postcue stimulus presentation (Fig. 4A). Because these trials did not involve postcue stimulus presentation or overt behavioral responses, the observed activation is unlikely to be explained by sensory processing or motor execution and instead reflects endogenous, stimulus-independent attentional signals. For comparison, activation maps from the stimulus-present contrasts are shown in Figure S2.

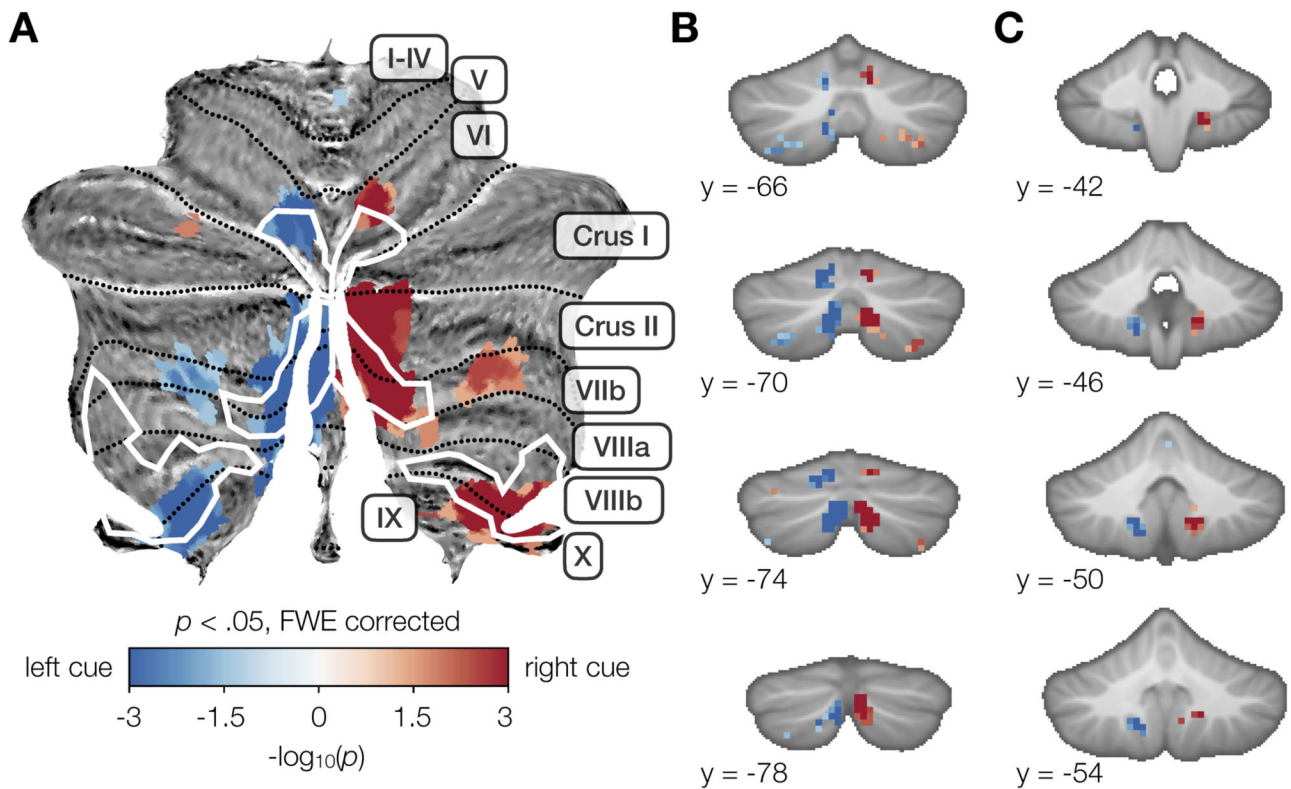


Figure 3. Multivariate feature weight mapping. **A**, Voxelwise statistical map from TFCE analysis of multivariate feature weights derived from a linear SVM trained to classify left- versus right-cue trials. Cool colors denote voxels whose classifier weights significantly contributed to left-cue classification, whereas warm colors denote voxels contributing significantly to right-cue classification. Values reflect corrected p values (TFCE with permutation testing, FWE controlled at $p < 0.05$). Significant voxels indicate clusters of reliable classifier contributions. The white contour outlines the cerebellar visual topographic map adapted from van Es et al. (2019). **B**, Volume-space visualization of significant clusters in Lobule VI and Crus II/VIIb/VIIIa shown in **A**. **C**, Volume-space visualization of significant clusters in Lobules VIIIb/IX/X shown in **A**.

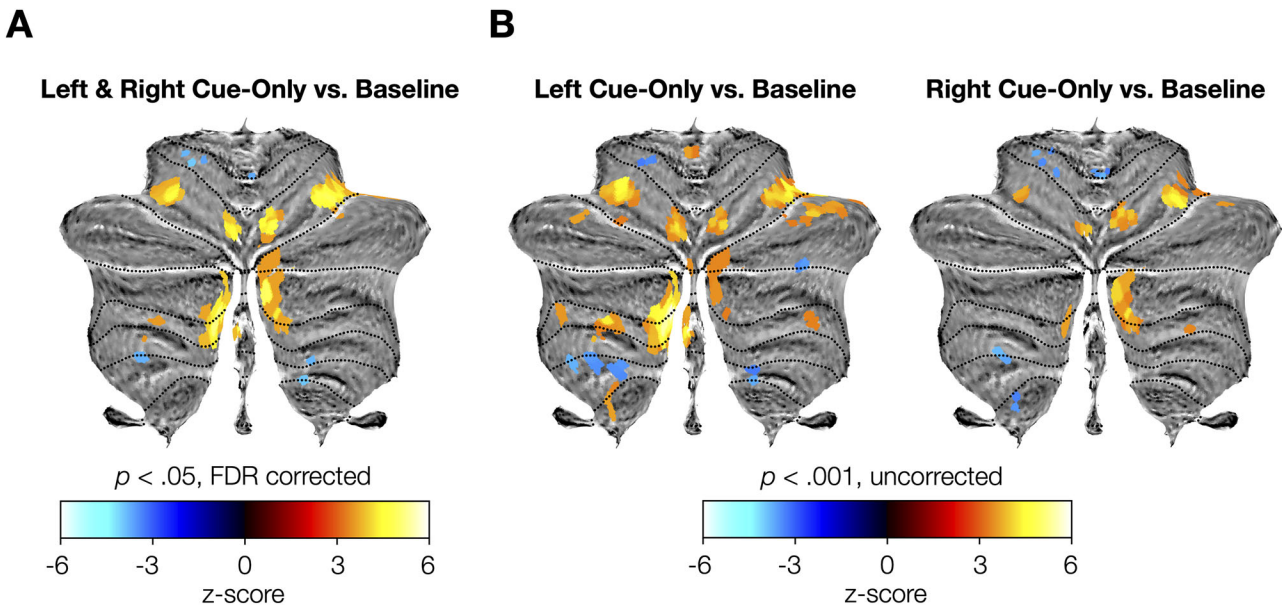


Figure 4. Cerebellar activation during attentional deployment in the absence of postcue stimulus presentation. **A**, Results of GLM testing the cue-only contrast of the attention task, combining left- and right-cue trials. The group-level z-map shows regions with significantly increased or decreased activation during cue-only conditions relative to baseline, thresholded at $p < 0.05$ (two-sided, FDR-corrected). **B**, Results of GLMs contrasting left-cue and right-cue conditions separately against baseline. Maps show regions with significantly increased or decreased activation during the respective cue-only condition, thresholded at $p < 0.001$ (two-sided, uncorrected).

In addition, lateral Lobule VI was significantly activated in the cue-only contrast despite not exhibiting spatially selective attentional coding (Figs. 3, 4A), indicating that this region is engaged by attentional state but does not represent the spatial locus of attention. In contrast, lateral Lobule VIIb and Lobules VIIIb/IX/X did not show significant modulation in the cue-only contrast, despite exhibiting spatially selective attentional coding.

To assess whether the observed stimulus-independent attentional modulation was spatially selective, we conducted separate GLMs contrasting left- and right-cue-only trials against baseline. These analyses revealed largely overlapping regions of activation by both cue directions (Fig. 4B), indicating that the identified regions are engaged during attentional deployment regardless of the attended hemifield. However, the magnitude and spatial extent of activation in these regions differed systematically between hemispheres, with stronger responses in the hemisphere ipsilateral to the attended hemifield. This hemispheric asymmetry is consistent with spatially biased attentional orienting within these regions. Together, these findings demonstrate that cerebellar activity reflects both spatially selective and nonspatial components of attentional control, with activity persisting even in the absence of postcue visual stimulation.

Attentional modulation in topographically organized cerebellar regions is stimulus-independent and contrast-invariant

We next asked whether attentional modulation in cerebellar regions exhibits properties characteristic of cortical visual areas, specifically whether it is invariant across stimulus contrast. To address this, we analyzed peak PSC in each ROI using LME models with cue direction, hemisphere of the ROI, and stimulus contrast as fixed effects. This approach also allowed us to assess whether spatially selective attentional modulation, previously identified using multivariate analyses, could also be revealed using a univariate approach. Effect sizes for fixed effects were quantified using partial eta squared (η_p^2), calculated from Type

Table 1. LME results for spatially selective and contrast-invariant attention effects

ROI	Cue Dir $\times$ Hemi			Cue Dir $\times$ Hemi $\times$ Contrast	
	$F_{(1,539)}$	p	η_p^2	$F_{(2,539)}$	p
Cortical ROIs					
V1	66.86	<0.001	0.11	0.51	0.600
MT+	55.32	<0.001	0.09	0.11	0.894
Cerebellar ROIs					
Medial Lobule VI	16.40	<0.001	0.03	0.26	0.771
Lateral Lobule VI	3.66	0.056	0.007	0.33	0.716
Medial Crus II/Lobule VIIb	40.58	<0.001	0.07	0.25	0.779
Lateral Lobule VIIb	3.92	0.048	0.007	0.03	0.969

F and *p* values are from Type III tests of fixed effects in LME models with subject as a random intercept. η_p^2 , partial eta squared; Cue Dir, Cue direction; Hemi, Hemisphere. Degrees of freedom were identical across ROIs. Effects in Lobules VIIIb/IX/X are not reported because hemispheric selectivity is enforced by the localization procedure.

III ANOVA tables. Cortical ROIs (V1 and MT+) were defined with their respective localizers, whereas cerebellar ROIs were defined primarily using the cue-only contrast from the attention task GLM (Fig. 4A). Although lateral Lobule VIIb is not visible in the thresholded group-level cue-only map, participant-specific ROIs could nevertheless be identified because ROI selection was performed using a more liberal threshold. In contrast, Lobules VIIIb/IX/X could not be reliably localized using the cue-only contrast and were therefore defined based on multivariate analysis results (Fig. 3). Because Lobules VIIIb/IX/X were not defined independently of the multivariate analysis, their peak PSC responses are shown for descriptive purposes only and are not statistically analyzed.

We first examined whether the cerebellar ROIs showed the same spatially selective and contrast-invariant attentional modulation observed in cortical visual areas. V1 and MT+ showed robust spatially selective attentional modulation, reflected in a significant cue direction $\times$ hemisphere interaction (Table 1). Critically, this interaction did not vary with stimulus contrast, as indicated by a nonsignificant cue direction $\times$ hemisphere $\times$ contrast interaction, consistent with the additive effects of

attention reported previously (Buracas and Boynton, 2007; Murray, 2008). A similar pattern was observed in cerebellar regions. Medial Lobule VI and medial Crus II/Lobule VIIb showed significant cue direction $\times$ hemisphere interactions, indicating spatially selective attentional modulation. Importantly, none of these regions showed a significant three-way interaction with contrast, demonstrating that attentional modulation was invariant across stimulus conditions, including in the absence of postcue stimulus presentation.

This additive effect of attention, observed in both cortical and cerebellar regions, is illustrated in Figure 5, where the separation between left-cue and right-cue response functions remains approximately constant across contrast levels. The parallel structure of these functions indicates that attentional modulation in these regions is additive rather than multiplicative, consistent with a stimulus-independent shift in response magnitude.

However, not all cerebellar regions exhibited this pattern. Lateral Lobule VI did not show a reliable cue direction $\times$ hemisphere interaction, consistent with its lack of spatial selectivity observed in earlier analyses (Table 1, Fig. 3). While lateral Lobule VIIb exhibited spatially selective attentional modulation in the multivariate analysis (Fig. 3), it showed only a weak cue direction $\times$ hemisphere interaction effect, suggesting that spatially selective information in this region is not strongly expressed at the level of area mean signal change. Likewise, Lobules VIIb/IX/X exhibited spatially selective attentional modulation in the multivariate analysis but were not reliably identified by the cue-only GLM contrast used for ROI definition (Fig. 4A). Although cue-only responses in these regions were above baseline, they were lower than those observed in the other cerebellar ROIs (Fig. 5). The relatively weak cue-only responses may have reduced the statistical sensitivity of the cue-only GLM, preventing reliable ROI localization.

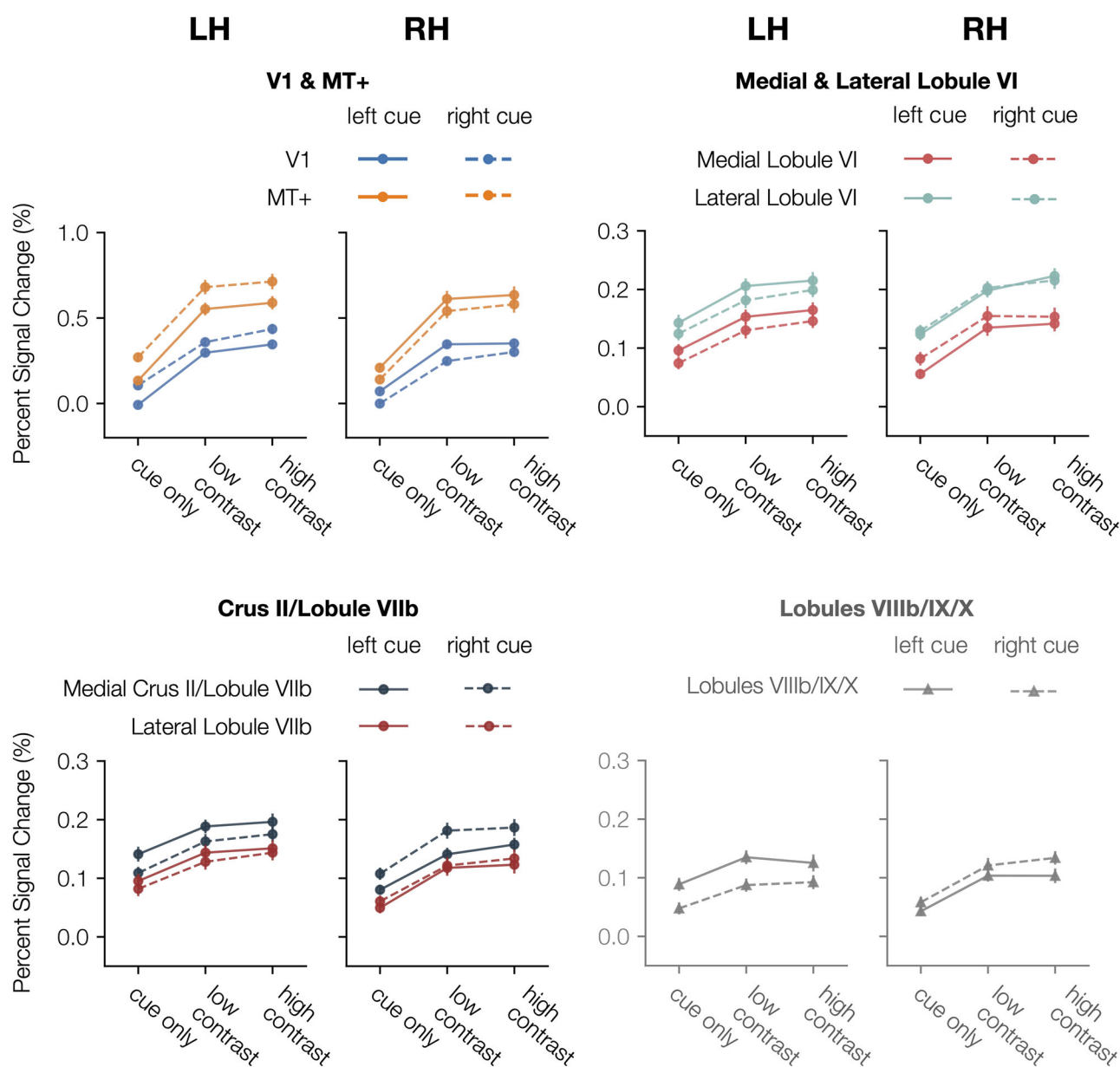


Figure 5. Contrast response functions in V1, MT+, and cerebellar visual areas. Peak PSC (y-axis) is plotted as a function of stimulus contrast (x-axis). Error bars indicate the standard error of the mean across 50 participants. Solid lines show PSC when attention was directed to the left visual hemifield (left cue), and dotted lines show PSC when attention was directed to the right visual hemifield (right cue). All ROIs except Lobules VIIb/IX/X were defined from the cue-only GLM result, whereas Lobules VIIb/IX/X (gray panel) were defined from the MVPA results because they did not show reliable activation in the cue-only contrast.

Table 2. LME model results for stimulus contrast and post hoc pairwise comparisons

ROI				Pairwise comparisons	
	Contrast			High–low contrast	
	$F_{(2,539)}$	p	η_p^2	Δ PSC	p
Cortical ROIs					
V1	390.68	<0.001	0.59	0.05	<0.001
MT+	451.27	<0.001	0.63	0.03	0.105
Cerebellar ROIs					
Medial Lobule VI	89.17	<0.001	0.25	0.01	0.371
Lateral Lobule VI	89.54	<0.001	0.25	0.02	0.038
Medial Crus II/Lobule VIIb	88.34	<0.001	0.25	0.01	0.146
Lateral Lobule VIIb	61.81	<0.001	0.19	0.01	0.251

F and p values for the main effect of contrast are from Type III tests of fixed effects in LME models with subject as a random intercept. η_p^2 partial eta squared. Post hoc pairwise comparisons between contrast levels were conducted using Tukey's test. Δ PSC, difference between estimated marginal means of peak PSCs. Some Δ PSC values appear identical due to rounding, but statistical tests were conducted on the underlying data, so corresponding p values differed. Effects in Lobules VIIIb/IX/X are not reported because this ROI was not defined independently.

Across all regions, PSC was greater during stimulus-present trials than during cue-only trials, resulting in a significant main effect of contrast (Table 2). However, contrast sensitivity differed across regions. V1 showed robust increases in activity with increasing contrast, whereas MT+ showed a weaker, nonsignificant trend. Among cerebellar regions, only lateral Lobule VI exhibited a modest contrast-dependent increase in activity, while other regions showed no reliable differences between low- and high-contrast conditions.

Together, these results demonstrate that cerebellar regions exhibiting spatially selective attentional modulation also show contrast-invariant, additive response profiles, closely paralleling key functional properties of attentional modulation in cortical visual areas.

Evaluation of potential eye-movement confounds

Eye movements are a potential confound in the interpretation of attention-related neural activity because they can alter both retinal input and activity within oculomotor regions. This issue is particularly relevant for cerebellar responses given the established role of the OMV/medial Lobule VI in eye-movement control. Overall, participants maintained fixation throughout the main experiment and localizers, with mean percentage of fixation time within 1° of visual angle from central fixation being 88.57% (SD = 13.52%, $N = 44$) during the attention task, 86.78% (SD = 17.90%, $N = 44$) during the V1 localizer, and 92.36% (SD = 11.31%, $N = 43$) during the motion localizer. However, fixation compliance alone does not rule out more subtle condition-dependent differences in eye-movement behavior that could influence activity in oculomotor regions. We therefore examined whether eye-movement behavior differed across experimental conditions and whether controlling for these differences altered the observed neural patterns.

We first assessed whether eye-movement behavior, specifically the total number of saccades and total saccade amplitude per trial, varied as a function of stimulus contrast. LME models predicting the two eye-movement measures from contrast, with subject included as a random effect, revealed a significant main effect of contrast on total saccade amplitude ($F_{(2,218)} = 16.03$, $p < 0.001$). Post hoc pairwise comparisons using Tukey's test showed that saccade amplitudes were significantly greater in high-contrast conditions than in either low-contrast (Δ total magnitude = 0.09°, $p < 0.001$) or cue-only conditions (Δ total

magnitude = 0.11°, $p < 0.001$), whereas low-contrast and cue-only conditions did not differ significantly (Δ total magnitude = 0.03°, $p = 0.358$). In contrast, the total number of saccades did not vary significantly with contrast ($F_{(2,218)} = 2.39$, $p = 0.094$). Thus, stimulus contrast influenced cumulative eye displacement but not the number of saccades.

We next examined whether cue direction systematically biased eye movements toward the attended visual hemifield. We quantified direction bias as the difference between the number or cumulative amplitude of leftward and rightward saccades. LME models revealed a significant effect of cue direction on directional bias in the number of saccades ($F_{(1,219)} = 17.98$, $p < 0.001$). Relative to left-cue trials, right-cue trials were associated with ~0.03 additional rightward-versus-leftward saccades per trial ($\eta_p^2 = 0.08$). In contrast, cue direction did not significantly predict direction bias in total saccade amplitude ($F_{(1,219)} = 0.05$, $p = 0.832$).

Taken together, these findings indicate that stimulus contrast and cue direction systematically influenced distinct aspects of eye-movement behavior. We therefore conducted an additional control analysis incorporating eye-tracking-derived nuisance regressors into the first-level GLM. Specifically, we included the average horizontal and vertical eye positions, total saccade amplitude, and the numbers of leftward and rightward saccades for each TR. These regressors were selected because they captured the aspects of eye-movement behavior that varied systematically across experimental conditions. We then compared beta estimates from the original and eye-movement-corrected GLMs within each participant's cerebellar ROIs, which were the same ROIs used in the univariate analyses. Beta estimates were compared using a LME model with fixed effects of GLM type (original vs eye-movement-corrected), ROI, and task contrast, with subject included as a random effect. No main effect of GLM type was observed ($F_{(1, 5,177)} = 1.49$, $p = 0.222$), indicating that inclusion of eye-movement nuisance regressors did not systematically alter the estimated task effects. Critically, there was no evidence that the impact of the eye-movement regressors differed across ROIs, as reflected by a nonsignificant GLM type $\times$ ROI interaction ($F_{(4, 5,177)} = 0.49$, $p = 0.745$). Likewise, neither the GLM type $\times$ task contrast interaction ($F_{(5, 5,177)} = 0.16$, $p = 0.976$) nor the GLM type $\times$ task contrast $\times$ ROI interaction ($F_{(20, 5,177)} = 0.02$, $p = 1.00$) reached significance, indicating that the inclusion of eye-movement nuisance regressors did not selectively alter beta estimates of specific task contrasts, whether across or within particular ROIs. These findings are notable because any influence of eye movements would be expected to be most prominent in OMV/medial Lobule VI.

To determine whether directional eye movements could account for the spatially selective attentional modulation observed in OMV/medial Lobule VI, we compared beta estimates associated with leftward and rightward saccades across cerebellar ROIs and hemispheres. Beta estimates were compared using a LME model with fixed effects of saccade direction, ROI, and hemisphere, with a random intercept for each subject. If the observed spatially selective attentional effects were driven by directional eye movements, leftward saccades would be expected to evoke stronger responses than rightward saccades in the left OMV, whereas rightward saccades would be expected to evoke stronger responses than leftward saccades in the right OMV. Such a pattern would result in a significant saccade direction $\times$ hemisphere interaction. However, neither the saccade direction $\times$ hemisphere interaction ($F_{(1,817)} = 0.04$, $p = 0.840$) nor the saccade direction $\times$ hemisphere $\times$ ROI interaction ($F_{(4,817)} = 0.35$, $p = 0.842$) was significant. Thus, although directional eye movements varied with cue direction, they did not produce spatially selective patterns of

cerebellar activity that differed across hemispheres or ROIs. These findings argue against the possibility that the patterns of spatially selective attentional modulation can be explained by systematic differences in leftward versus rightward eye movements.

In summary, these findings indicate that although eye movements varied systematically across experimental conditions, they are unlikely to account for the observed cerebellar effects. Incorporating eye-movement measures into the first-level GLM did not alter the estimated task responses, and directional saccades did not produce the hemisphere-dependent activation pattern expected if they were responsible for the observed spatially selective attentional modulation.

Functional heterogeneity of attentional and sensory signals within cerebellar visual representations

We next asked whether cerebellar regions that exhibit attentional modulation also participate in sensory processing or whether attentional and sensory signals are functionally dissociable within cerebellar representations of visual space. In cortical visual areas, such as V1 and MT+, attention modulates regions that are also strongly driven by sensory input. Whether a similar relationship exists in the cerebellum remains unclear.

To address this, we compared cerebellar responses associated with attentional deployment in the cue-only condition and motion-evoked sensory processing. The analysis was restricted to voxels that exhibited spatially selective attentional modulation according to the MVPA (Fig. 3). Sensory responses were localized using a motion localizer, and we quantified the relative contribution of attentional and sensory signals at each voxel using a bias index defined as the difference between group-level z statistics from the attention and motion GLM contrasts. Positive values indicate a bias toward attentional modulation, whereas negative values indicate stronger sensory responses.

Within cerebellar regions exhibiting spatially selective responses, we observed systematic differences in the relative contribution of attentional and sensory signals (Fig. 6). Medial Lobule VI and lateral Lobule VIIb showed an overall bias toward attentional processing, whereas other regions exhibited mixed or graded profiles. In medial Crus II/Lobules VIIb/VIIIa, a superior subregion was biased toward attentional processing, while a more inferior region was biased toward motion-related sensory responses, indicating a functional gradient along the superior–inferior axis. A similar gradient was observed in Lobules VIIIb/IX/X, where anterior regions were more biased toward sensory processing and posterior subregions were biased toward attention.

To characterize these spatial patterns, we constructed probability density functions of attention- and motion-biased voxels along the MNI axes. Specifically, we examined distributions along the Z -axis for medial Crus II/Lobules VIIb/VIIIa and along the Y -axis for Lobules VIIIb/IX/X (Fig. 6B). Each curve represents the estimated probability density of voxel coordinates along the anatomical axis. Higher values therefore indicate coordinates where voxels from a given population are more likely to be found. The resulting distributions again reveal a superior–inferior shift of functional bias in medial Crus II/Lobules VIIb/VIIIa and an anterior–posterior shift of bias in Lobules VIIIb/IX/X.

To further validate the idea that attention-modulated and motion-sensitive cerebellar regions are largely distinct, we examined the responses of attention-modulated ROIs during the motion localizer. Attention-modulated ROIs were the same ROIs defined in the previous LME analyses. One-sample t tests revealed that peak PSC values in attention-modulated medial and lateral Lobule VI, lateral Lobule VIIb, and Lobules VIIIb/IX/X during the motion localizer did not significantly differ from zero in either hemisphere (all $|t_{(49)}| < 1.05$, all $p > 0.300$,

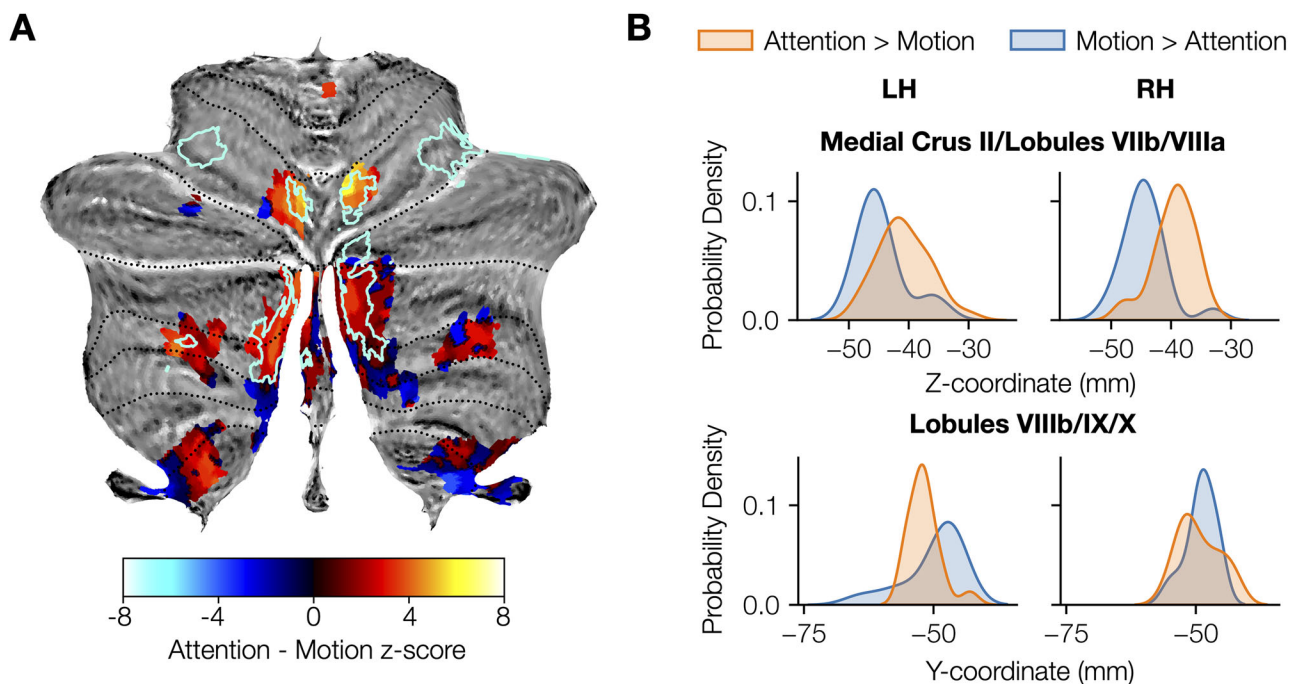


Figure 6. Relative contributions of attentional and sensory processing within cerebellar spatial representations. **A**, Flatmap visualization of the voxelwise bias index within cerebellar regions exhibiting spatially selective responses. The bias index was computed as the difference between z -statistics from the cue-only attention and motion GLM contrasts. Cyan contours denote statistically significant attention-modulated clusters identified in the cue-only analysis (Fig. 4A). **B**, Probability density functions of attention-biased and motion-biased voxel coordinates along the relevant MNI axes. Each curve represents the normalized spatial distribution of voxel locations.

two-sided). In contrast, activity in medial Crus II/Lobule VIIb differed significantly from 0% in the right hemisphere, although minimal in magnitude (mean PSC = 0.07%; $t_{(49)} = 4.24$, $p = 0.001$, Bonferroni-corrected), but not in the left hemisphere (mean PSC = 0.04%, $t_{(49)} = 1.63$, $p = 0.111$). While limited activation was observed in right medial Crus II/Lobule VIIb, the overall pattern indicates that cerebellar regions engaged during the deployment of covert spatial attention are largely distinct from those involved in sensory processing of moving visual stimuli.

Discussion

A growing body of neuroimaging evidence has implicated the cerebellum in visual attention, challenging the traditional view that its role is restricted to motor control. Early neuroimaging demonstrated that visual selective attention recruits cerebellar regions distinct from those involved in hand movements, suggesting that cerebellar activation during attention cannot be explained solely by motor demands (Allen et al., 1997). Later work identified a cerebellar node of the dorsal attention network (Kellermann et al., 2012; Brissenden et al., 2016) and subsequently demonstrated ipsilateral visual representations and spatially selective attentional signals in cerebellar Lobules VIIb/VIIIa (Brissenden et al., 2018). Together, these findings suggested that the cerebellum contributes to visual attention. However, the subsequent discovery of additional topographically organized visual representations throughout the cerebellum (van Es et al., 2019) raised the question of whether spatially selective attentional signals extend beyond Lobules VIIb/VIIIa and whether cerebellar attentional responses share key functional characteristics with those observed in cortical visual areas. Here, we show that spatially selective attentional signals are present across multiple cerebellar visual representations, extending beyond the originally described VIIb/VIIIa region. We also show that attentional modulation in the cerebellum is not uniform but instead exhibits both spatially selective and non-spatial components, as well as graded differences in the relative contribution of attentional and sensory signals across cerebellar regions. Our findings also indicate that attentional modulation in the cerebellum exhibits functional properties that closely parallel those observed in cortical visual areas.

Spatially selective attentional coding in the cerebellum

Our MVPA results demonstrated that cerebellar activity contained information about the attended hemifield, extending previous findings of spatially selective attentional signals in Lobules VIIb/VIIIa (Brissenden et al., 2018) to additional cerebellar visual representations identified by van Es et al. (2019). Although some regions showed stronger multivariate than univariate effects, together these analyses indicate that information about attentional locus is distributed across multiple cerebellar visual regions. The close spatial correspondence between cerebellar regions representing the spatial locus of attention and previously described visual representations suggests that attentional modulation largely operates within established cerebellar representations of visual space, consistent with the organization of cortical visual areas, where attentional modulation is spatially linked to retinotopic organization (Brefczynski and DeYoe, 1999).

Although the observed attentional effects largely coincided with previously described cerebellar visual representations, the correspondence was not complete. In Lobules VIIIb/IX/X, the attention-sensitive region occupied only a subset of the retinotopic map reported by van Es et al. (2019). One possible explanation is methodological. Whereas van Es et al. (2019) localized visual representations using dedicated retinotopic mapping in a

substantially larger Human Connectome Project retinotopy dataset, the present study identified regions exhibiting attentional modulation in a smaller sample. Consequently, the current analyses may have detected only a subset of the underlying visual representation exhibiting sufficiently robust attentional responses. Alternatively, the partial overlap may reflect functional heterogeneity within the VIIIb/IX/X visual representation, suggesting that only a subset of this map participates in spatially selective attentional processing. Conversely, we also identified spatially selective attentional signals in lateral Lobule VIIb, a region not included within the visual representations reported by van Es et al. (2019). Future studies combining retinotopic mapping and attentional paradigms within the same participants will be necessary to determine whether these differences reflect limitations in current visual maps or task-dependent recruitment of certain cerebellar regions.

Another important consideration in interpreting cerebellar activity during visual attention tasks is whether the observed responses reflect attentional processing itself or instead arise from accompanying eye movements or other motor-related processes, a concern that has been raised in many previous studies (Corbetta et al., 1998; Gitelman et al., 1999; Bischoff-Grethe et al., 2002). In this study, we took several steps to minimize potential contributions from eye movements and motor responses. First, the univariate analyses localized cerebellar regions exhibiting attentional modulation using cue-only trials, thereby isolating attentional orienting from button presses. Second, although eye-tracking data revealed subtle condition-dependent differences in eye-movement behavior, these differences were insufficient to account for the observed neural responses. Incorporating eye-movement regressors into the GLM analysis produced highly similar activation profiles, indicating that the attentional effects persisted after accounting for oculomotor behavior. These findings are also consistent with recent work suggesting that activity within the OMV/medial Lobule VI cannot be explained by saccadic eye movements alone. King et al. (2019) reported that simple saccadic eye movements elicited little activation in OMV, whereas robust responses during visual search were observed in OMV even after accounting for the number of saccades performed. Together with the present findings, these results suggest that OMV activity is not solely determined by eye movements but is also modulated by cognitive task demands.

Additive attentional modulation and contrast sensitivity in the cerebellum

A central finding of the present study is that attentional modulation in cerebellar regions was largely invariant across stimulus contrast, consistent with an additive, stimulus-independent shift in response magnitude. This pattern closely parallels attentional effects observed in cortical visual areas, where additive increases in BOLD activity are thought to reflect stimulus-independent top-down bias signals superimposed on sensory responses (Buras and Boynton, 2007; Li et al., 2008; Murray, 2008; Sylvester et al., 2009).

We replicated this additive effect in cortical visual areas V1 and MT+ and further demonstrated a similar pattern in cerebellar regions, including medial Lobule VI, medial Crus II/Lobule VIIb, and lateral Lobule VIIb, indicating that cerebellar attentional modulation shares a key functional property of cortical visual attention. Because cerebellar hemodynamic responses are suggested to primarily reflect synaptic activity within the mossy fiber-granule cell system rather than Purkinje cell output (Iadecola et al., 1997;

Attwell and Iadecola, 2002; Diedrichsen et al., 2019), the observed additive effects likely reflect top-down attentional signals conveyed through corticocerebellar pathways and their subsequent processing within the cerebellar cortex. However, additive BOLD responses do not necessarily imply a unique neural mechanism, as similar effects can arise in the cerebral cortex through population averaging or nonlinear vascular dynamics (Hara et al., 2014; Liu et al., 2021). Whether these mechanisms generalize to the cerebellum remains unknown.

Only a subset of regions examined in the current study exhibited sensitivity to stimulus contrast itself. As expected, V1 responses were greater for high- than low-contrast stimuli, consistent with previous findings of contrast sensitivity in the early visual cortex. An unexpected finding was the presence of contrast sensitivity in lateral Lobule VI, a region not previously associated with visual topographic organization (van Es et al., 2019). Given the modest difference in response magnitude ($\Delta\text{PSC} = 0.02$, $p = 0.038$), this finding should be interpreted cautiously. Future work using tasks that more directly dissociate sensory drive from attentional or other cognitive processes will be necessary to determine whether lateral Lobule VI exhibits genuine contrast sensitivity. At the same time, the apparent absence of contrast sensitivity in other cerebellar regions may reflect methodological rather than functional differences. Physiological noise contributes substantially to signal fluctuations in cerebellar fMRI (Van Der Zwaag et al., 2015), potentially reducing sensitivity to detect subtle contrast-dependent effects.

Functional heterogeneity across the cerebellar cortex

In addition to spatially selective attentional representations, our results reveal substantial functional heterogeneity across the cerebellar cortex. Lateral Lobule VI exhibited increased activity during attentional orienting that did not significantly differ between attended hemifields, suggesting that this region contributes to the allocation of attention without representing its spatial locus. This finding is consistent with previous work implicating lateral Lobule VI in perceptual and cognitive demands rather than simple sensory processing (Baumann and Mattingley, 2014). Because this region was also recruited during cue-only trials, its activity cannot be attributed to postcue sensory responses and instead likely reflects top-down attentional processes.

Functional heterogeneity was also evident within spatially selective regions. Spatially selective modulation in lateral Lobule VIIb was weaker than in other cerebellar visual regions, consistent with previous evidence for a functional gradient within Lobule VIIb/VIIIa, in which dorsal-medial regions are more strongly associated with spatial coding and ventral-lateral regions with visual working memory load (Brissenden et al., 2018). More broadly, comparisons between attentional and motion-related responses revealed systematic gradients in the relative contribution of attentional and sensory signals in medial Crus II/Lobules VIIb/VIIIa and Lobules VIIIb/IX/X. Rather than forming discrete functional subdivisions, neighboring subregions exhibited gradual transitions in attentional and sensory preference, broadly consistent with prior work demonstrating that the cerebellum exhibits heterogeneous functional profiles and connections to cerebral functional networks (Buckner et al., 2011; Guell et al., 2018; King et al., 2019; Xue et al., 2021). These findings underscore that cerebellar functional organization is not strictly segregated and that individual subregions may contribute to multiple cognitive processes beyond those isolated in the present study.

Together, these findings indicate that cerebellar visual representations are functionally heterogeneous, differing both in whether they represent the spatial locus of attention and in the relative contribution of attentional and sensory processing.

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