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Cerebellar Response to Familiar and Novel Stimuli: An fMRI Study

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Historically known for its key contribution to motor behavior, the cerebellum continues to break boundaries. Researchers have demonstrated the cerebellum also plays a role in learning, memory, and more recent evidence for contributions in language, attention, working memory, emotions, and social processes. Here, we present a study that adds to the list of nonmotor processes of the cerebellum. We used images of faces and outdoor scenes to examine the cerebellar response to familiar and novel stimuli. Participants were familiarized with a subset of stimuli, and then underwent functional MRI (fMRI) where they were presented with the previously stimuli and new stimuli while making “old” and “new” judgment. In a familiar versus novel contrast, familiar stimuli (faces and scenes combined) activated bilateral regions of the cerebellum including I–IV, V, VI, Crus I, and Crus II. When separated by type, familiar faces had greater activation of bilateral I–IV than novel faces. These results demonstrate the cerebellar role in determining familiarity and contribute to continuing research supporting cerebellar contributions to nonmotor processes.

Keywords: cerebellum, faces, scenes, familiar, novel

The function of the cerebellum has been expanded and revised since its establishment as a modulator of motor behaviors. The first major amendment took place over the latter portion of the 20th century, when Thompson and colleagues presented a body of work demonstrating that the interpositus nucleus of the cerebellum was central in the acquisition and retention of classically conditioned motor responses (Christian & Thompson, 2003; McCormick & Thompson, 1984; Swain & Thompson, 1993; Thompson, 1976, 1986). Their claim that the cerebellum could show plasticity and store memory was met with early controversy, but is now widely accepted. Recently, a second revision goes beyond motor behavior and memory to suggest that the cerebellum may play a modulatory role in nonmotor cognitive and executive processes. The current article provides additional support for the cerebellum in the recognition of familiar stimuli.

Anatomical and functional neuroimaging methods indicate that the cerebellum may contribute to more than just motor behavior. The cerebellum, containing a well-defined functional topography, is in a position to modulate a wide variety of cognitive and motor behaviors (Stoodley, Valera, & Schmahmann, 2012; Strick, Dum, & Fiez, 2009). Using retroviral tract tracing methods, Strick and colleagues were able to demonstrate that the dentate nucleus of the cerebellum has connections with motor and premotor regions of the cerebral cortex including areas of the motor cortex, premotor cortex, prefrontal cortex, and parietal cortex (Dum & Strick, 2003; Kelly & Strick, 2003; Strick et al., 2009).

Evidence from neuroimaging studies of the cerebellum provides further support for cerebellar contributions to cognition. Studies of resting-state functional connectivity between the cerebellum and nonmotor networks consistently report correlations between cerebellar subregions of Crus I, Crus II, and lobule VI and executive, salience, and default mode networks (Buckner, 2013; Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Caulfield, Zhu, McAuley, & Servatius, 2016; Habas et al., 2009). Examinations of resting-state functional connectivity of the sensorimotor network indicate distinctly different regions of correlating activity in the cerebellum including I–IV and V, as well as some overlapping regions (lobule VI) which may indicate a key role for sensory integration in subregions of the cerebellum (Kipping et al., 2013;

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O'Reilly, Beckmann, Tomassini, Ramnani, & Johansen-Berg, 2010). Additional support comes from task-based functional MRI (fMRI) studies. In their study, Stoodley and colleagues (2012) used fMRI to examine cerebellar activations during active movement compared with tasks of language, spatial processing, and working memory. Overt movement activated lobules IV–V and VIII, whereas nonmotor tasks activated voxels within lobule VI (verb generation, working memory), Crus I (verb generation), VIIB–VIIIA (verb generation), VII (mental rotation, working memory). Other studies looking at cerebellar activations during specific cognitive tasks include reports of cerebellar contributions during sensory processing, attention, verbal working memory, emotion, and social cognition (Hayter, Langdon, & Ramnani, 2007; Kirschen, Chen, & Desmond, 2010; Koziol, Budding, & Chidekel, 2012; Marvel & Desmond, 2010; Moberget et al., 2008; Stoodley et al., 2012; Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014).

It is widely accepted that the cerebellum engages in sensory prediction. The cerebellum monitors incoming stimuli for a mismatch between the expected and reality (Ivry, 2000; Nixon, 2003). In motor behavior, this feedback loop is used to adjust motor actions, enabling coordinated and smooth actions (Brooks & Thach, 1981; Ito, 1984; Marr, 1969). It is possible that motor sensory prediction may also apply to prediction of visual stimuli, enabling the cerebellum to engage in a process of multisensory integration, detecting environmental changes, and communicating to the cortex to regulate cognition and action (Molinari & Leggio, 2007). Accordingly, the presentation of visual stimuli may engage the cerebellum, preparing the body for motor behavior, with activity changes reflecting processes of sensory prediction and integration. Here, we used task-based functional MRI to examine cerebellar activity, with the prediction that specific regions of the cerebellum would be differentially activated by familiar and novel stimuli.

Materials and Method

Participants

Twenty-six students (19 females and 7 males, mean age 20.65, range 18–25) from a large midwestern state university participated. The research procedure, consent forms, and study materials were in accordance with the ethical standards of the American Psychological Association and were approved by the Michigan State University Biomedical and Health Institutional Review Board (Protocol 11–015). All participants signed informed consent before study procedures began.

Stimuli

Stimuli were 96 full-color digitized photographs. Face stimuli were of neutral expression faces of male and female adults from the AR face database (Martinez & Benavente, 1998) and scene stimuli were color images taken from typical rooms in a home (e.g., living room, kitchen, office, etc.) that were used in a previous imaging study (Henderson, Larson, & Zhu, 2007). The fixation cross was a 1-in. × 1-in. "+" sign in black placed in the center of a white background.

Familiarization Procedure

Familiarization to a subset of stimuli (24 faces, 24 scenes) took place outside of the scanner at least 1 and no more than 3 days prior to functional MRI scanning. Participants were shown faces and scenes on a computer monitor for 1 s each in randomized blocks (e.g., randomly presented faces, then randomly presented scenes) controlled by E-Prime (Psychology Software Tools, Inc., Pittsburgh, PA). Each photo was shown once per block (48 images per block), and each block was repeated six times, totaling six 1-s presentations of each image. Face and scene groups were counterbalanced between participants.

Imaging Procedure

In the scanner, instructions presented on the screen informed participants that they would see images from the familiarization day and new images. They were given a response pad and instructed to use their thumb to indicate "old" and their forefinger to indicate "new" in response to each stimulus while it was presented. Instructions were self-paced and participants were asked to make each type of response before proceeding.

A rapid event-related design paradigm was controlled by a computer equipped with E-Prime (Psychology Software Tools, Inc., Pittsburgh, PA). The visual stimuli were presented on a 1024 × 768, 32-in. LCD monitor. The experiment was divided into four functional runs each lasting 7 min. In each run, baseline conditions and stimulus trials (6 per condition, 24 total stimuli per run) were pseudorandomly arranged using the RSFgen program in AFNI software (Cox, 1996) for optimizing the calculation of the hemodynamic response function for each stimulus condition. Each stimulus was presented for 2.5 s, so that it fit with the time of repetition (TR) in the pulse sequence, with fixation intervals varying between 0 and 27.5 s. Participants were instructed to use the keypad to make the "old"/"new" response during each stimulus presentation.

MRI Acquisition

The MRI experiment was conducted on a GE 3T Signa HDx MR scanner (GE Health care, Waukesha, WI) with an 8-channel head coil. During each session, first and higher-order shimming procedures were carried out to improve magnetic field homogeneity. Four runs of 7-min. echo-planar imaging data sets, starting from the most inferior regions of the cerebellum, were acquired with the following parameters: 44 contiguous 3-mm axial slices in an interleaved order, time of echo (TE) = 20 ms, time of repetition (TR) = 2,500 ms, parallel acceleration factor = 2, flip angle = 80°, field of view (FOV) = 22 cm, matrix size = 64 × 64, ramp sampling, and with the first four data points discarded. After the functional data acquisition, 180 T_1-weighted 1-mm^3 isotropic volumetric inversion recovery fast spoiled gradient-recalled images (10-min. scan time), with cerebrospinal fluid (CSF) suppressed, were obtained to cover the whole brain with the following parameters: TE = 3.8 ms, TR of acquisition = 8.6 ms, time of inversion (TI) = 831 ms, TR of inversion = 2332 ms, flip angle = 8°, FOV = 25.6 cm × 25.6 cm, matrix size = 256 × 256, slice thickness = 1 mm, and receiver bandwidth = ± 20.8 kHz.

Neuroimaging Data Analysis

Neuroimaging data preprocessing. All fMRI data preprocessing and analysis was conducted with AFNI software (Cox, 1996). For each participant, acquisition timing differences was first corrected for different slice locations. With the last functional image as the reference, rigid-body motion correction was done in three translational and three rotational directions. The magnitude of movements in these six directions was estimated and then these estimates were used in the "3dDeconvolve" process described next. Spatial blurring with a full width half maximum (FWHM) of 4 mm was applied to reduce random noise and intersubject anatomical variation during group analysis.

For each participant, the impulse response function (IRF) was resolved with multiple linear regressions at each voxel with respect to each stimulus condition (including four conditions with correct trials and four conditions with incorrect trials) using the 3dDeconvolve routine in AFNI (Ward, 2000). The IRFs were resolved to 7 points from 0 to 15 s at the resolution of 2.5 s (time of repetition). The BOLD signal change was calculated on the basis of the area under the IRF curve. The percent signal change for each participant at each stimulus condition was processed in the native space with a voxel size of 3.44 mm × 3.44 mm × 3 mm after the 4-mm FWHM space blurring. General linear tests were applied on a voxel-wise basis for each of the stimulus conditions at the correct trials to inspect brain activation on individual subjects.

Whole-brain analysis. To avoid difficulties in cerebellar registration to standard space, individual brain activation maps were coregistered to the MNI305 template space using the FreeSurfer nonlinear registration pipeline (Fischl et al., 2002). This procedure verified that the cortical and subcortical regions, as well as the cerebellum, could be normalized to the standard space with a high level of accuracy, and has been successfully applied in Alzheimer's research (Zhu, Majumdar, Korolev, Berger, & Bozoki, 2013). Additional spatial blurring (2-mm FWHM) was applied after warping to the MNI305 template space to reduce the noise due to the nonlinear warping of the percent signal changes from the native space to the MNI 305 space. This process was applied successfully in prior work by Zhu et al. (2013). A mixed-effects analysis of variance (ANOVA) was then performed over the entire (n = 26) data set with stimulus condition (four types (all in correct trials): familiar face, novel faces, familiar scene, novel scene) as the fixed effect and participant as the random effect. ANOVA results were used to extract the differentially active voxels for all contrasts.

Monte Carlo simulation was performed according to the matrix and voxel size of the imaging volume, voxel intensity thresholding, masking and spatial smoothness of image data inherited and applied. The spatial smoothness of image data was estimated based on "3dFWHMx" in AFNI (Cox, 1996). The cluster analysis was used to estimate the overall statistical significance with respect to the whole brain (Ward, 2000). The statistical results were corrected for multiple comparisons based on the following criteria: A voxel was considered significant only if it was within an 1170 mm^3 cluster in which the voxels were connected and all had a voxel-based $p \leq .005$. Based on the application of these criteria to the whole brain, the voxel-based $p \leq .005$ was corrected to be an equivalent whole-brain corrected $p \leq .047$.

Cerebellar structural and thresholded functional data were isolated and normalized into standard stereotaxic space using the spatially unbiased atlas template (SUIT) of the human cerebellum (Diedrichsen, 2006) for visual presentation of statistically significant cerebellar clusters. Tables derived from the SUIT template do not include MNI coordinates as the correspondence between standard MNI 305 standard space and SUIT atlas space is not precise.

Results

Behavioral Results

Reaction times for responses to stimuli were measured in milliseconds. A 2 (stimulus: face/scene) × 2 (familiarity: familiar/novel) mixed effects ANOVA revealed a significant interaction of stimulus by familiarity, $F(1, 25) = 10.435$, $p = .003$. Follow-up Bonferroni corrected pairwise t tests indicated that the interaction was driven by differences between the familiar face and familiar scene stimuli, $t(25) = -6.568$, $p < .001$, and between the familiar scene and novel face stimuli $t(25) = 3.355$, $p = .003$. Corrected recognition scores (d': hit rate—false alarm rate) were not significant for faces and scenes, all p's > .705. Participants were able to recognize previously familiarized stimuli and correctly reject new stimuli with overall accuracy of 81%. The best recognition accuracy was for novel stimuli with 86% recognition accuracy for novel faces and 85% recognition accuracy for novel scenes. Recognition accuracy was lower for familiar stimuli, with 81% for familiar faces and 77% for familiar scenes (see Table 1). One-way ANOVAs to examine between-groups differences in recognition accuracy revealed a significant difference between sexes on accuracy of scene stimuli, $F(1, 24) = 4.457$, $p = .045$, but not for faces ($p = .358$). Examination of recognition accuracy indicates that the female participants were better at both scenes and faces with a recognition accuracy of 80% and 79% respectively, compared with the males 70% (scenes) and 73% (faces).

Parahippocampal place area and fusiform face area. First, to ensure that our stimuli were being processed as expected we extracted percent signal change from baseline for each stimulus

Table 1
Demographic and Behavioral Results by Group

Measure	Mean (*SD*)
Demographics	
Sex (females)	26 (19)
Age	20.7 (1.9)
Education	14.7 (1.8)
Mean reaction times	
Familiar faces	1,168.7 (119.7)
Familiar scenes	1,294.0 (132.8)
Novel faces	1,224.9 (144.7)
Novel scenes	1,235.9 (158.7)
Recognition accuracy	
Familiar faces	81% (14.3%)
Familiar scenes	77% (14.0%)
Novel faces	86% (12.2%)
Novel scenes	85% (11.9%)
Corrected recognition (d')	
Faces	2.4 (0.8)
Scenes	2.5 (0.8)

type in regions of interest for processing faces, the fusiform face area (FFA; (Kanwisher, McDermott, & Chun, 1997) and for processing scenes, the parahippocampal place area (PPA; (Henderson et al., 2007). Both PPA and FFA were functionally defined using the whole-brain statistical threshold, but with restriction to the corresponding anatomically boundaries. Bilateral parahippocampi and fusiform gyri were located in the Talairach space (Talairach & Tournoux, 1988). Statistically significant scene-selective PPA activation was defined by the group-level contrast of (scenes–faces) at a voxel-based $p < .001$ within parahippocampal anatomical boundaries. Similarly, the FFA was defined based on the Group ANOVA of [face-scene] and thresholded at voxel-based $p < .001$ within bilateral fusiform face area boundaries. BOLD % signal change values were averaged for the left and right PPA, and left and right FFA. A 2 (stimulus: face/scene) × 2 (region: FFA/PPA) repeated measures ANOVA revealed a significant Stimulus × Region interaction, $F(1, 25) = 5.322$, $p < .001$, such that percent signal change from baseline is greater at the FFA for faces and at the PPA for scenes.

Cerebellum specific responses to stimuli. To assess if the cerebellum was differentially responsive to familiar and novel stimuli in general, we collapsed activity over faces and scenes. We found that the cerebellum was significantly more active to familiar stimuli than novel in the vermis and areas of the left and right cerebellar hemispheres (Table 2, Figure 1). Next, to see if faces or scenes were specifically processed in the cerebellum we examined responses to familiar compared with novel for faces and scenes separately. Only the contrast for familiar and novel faces revealed cerebellar activity, with significantly greater response of the bilateral region I–IV to familiar faces than novel faces (Figure 2). Exploratory examination with a reduced threshold of $p < .005$ and cluster size of 100 voxels revealed similar patterns of activation for the familiar scene group, with increased activity in the vermis and bilateral I–IV, as well as activations spanning bilateral Crus I, Crus II, and VIII that were not observed with the faces, suggesting that the shared region of the vermis and I–IV may be more specialized for familiarity, whereas other regions of the cerebellum may be activated for specific stimulus content.

Table 2
Significant Cerebellar Activations for Contrasts Between Stimulus Types

Max *t* value	Cerebellum region
Familiar > Novel	
5.255	Vermis VI
5.883	Left I–IV
5.180	Right I–IV
4.340	Right V
4.297	Left V
5.920	Right VI
5.558	Left VI
4.867	Right crus II
4.637	Left crus II
4.659	Left crus I
5.889	Right cus I
Familiar face > Novel face	
4.032	Right I–IV
4.080	Left I–IV
Familiar scene > Novel scene	No clusters

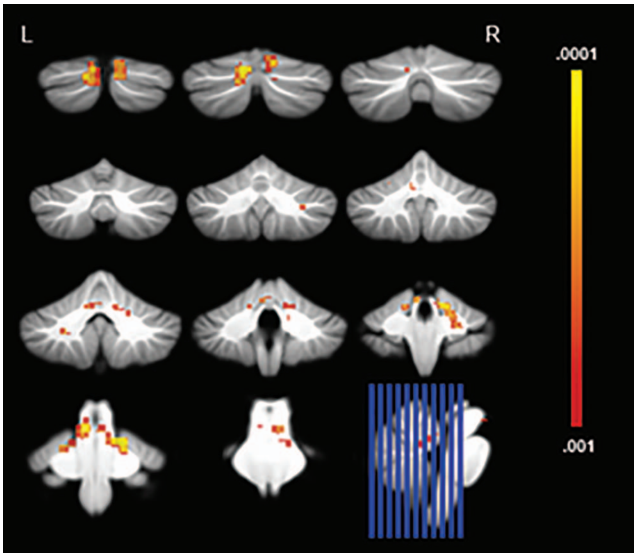

Figure 1. Familiar > novel. Regions of significantly greater activity to familiar stimuli compared with novel stimuli in the cerebellum. Regions of activity in the cerebellum included the vermis and bilateral activations in the I–IV, V, VI, Crus I, and Crus II. The bar indicates *p* value. See the online article for the color version of this figure.

Whole brain responses to stimuli. We repeated this process for the whole brain responses. First, we contrasted familiar and novel overall (collapsing across faces and scenes), and found that there was significantly greater activity in the left inferior parietal lobule and left middle frontal gyrus for the familiar stimuli (see Table 3). There were no areas with greater activity for novel stimuli. Then, we examined faces and scenes separately. For

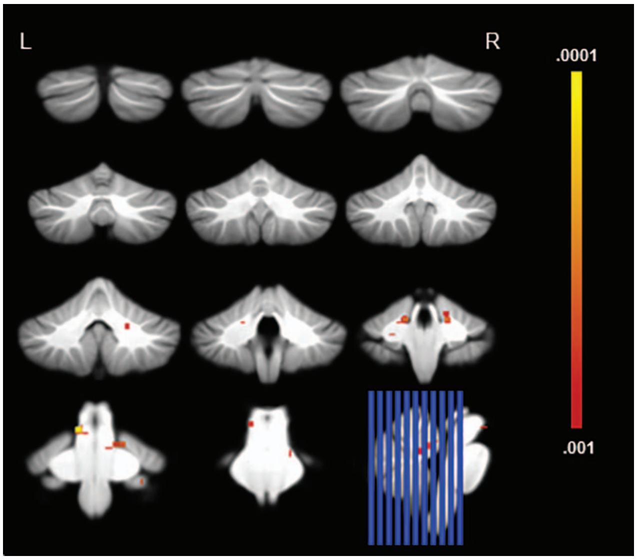

Figure 2. Familiar faces > novel faces. Regions of significantly greater activity to familiar face compared with novel face stimuli. Significant increases in cerebellar activity to familiar faces in the right and left lobule I–IV. The bar indicates *p* value. See the online article for the color version of this figure.

Table 3
Significant Cerebral Activations for Contrasts Between Stimulus Types

Max *t* value	Brain region	MNI coordinates (*X Y Z*)
Familiar vs. novel		
5.706	Left inferior parietal lobule	−36, −57, 41
5.101	Left middle frontal gyrus	−47, 7, 42
Familiar faces vs. novel faces		
4.297	Right posterior cingulate	17, −45, 7
Familiar scenes vs. novel scenes		
8.566	Left lingual gyrus	−1, −89, −19
6.032	Left precuneus	−28, −65, 38
5.591	Right precuneus	15, −66, 17
5.218	Left middle frontal gyrus	−49, 10, 43

familiar compared with novel faces, there was greater activity in the right posterior cingulate. For the familiar compared with novel scene contrast we found greater activity in the left lingual gyrus, left middle frontal gyrus, and bilateral precuneus.

Discussion

Due in large part to the work of Richard Thompson and his colleagues, it is now widely accepted that the cerebellum is essential in the learning and memory of classical eyeblink condition. In the spirit of further understanding the function of the cerebellum, the present study presents an extension of cerebellar functioning to old and new judgments of faces and scenes. To do this, we examined a contrast of familiar versus novel stimuli including faces and scenes. We found increased cerebellar activity to familiar compared with novel stimuli spread across areas of the cerebellum including the vermis, and bilateral hemispheres.

Thus far, little research has been done to specifically examine the response of the cerebellum to familiar and novel stimuli, resulting in conflicting support for cerebellar contributions to processing novel stimuli (Murty, Ballard, Macduffie, Krebs, & Adcock, 2013), and familiar stimuli (Maddock, Garrett, & Buonocore, 2001; Platek et al., 2006; Yonelinas, Otten, Shaw, & Rugg, 2005), and in some cases, to both novel and familiar stimuli in the same study (Kim et al., 1999). As researchers examine the specific role the cerebellum has in nonmotor processes, it is essential to examine its role in the processing of familiar and novel.

When we collapsed responses across faces and scenes, combining the two for more power, we found that cerebellar activity increases more in response to familiar than novel stimuli. Clusters of activity across the cerebellum indicate a distributed network responsive to familiarity. Activity observed in lobules VI, Crus I, and Crus II support previous research implicating these areas in nonmotor processes (Kerren-Happuch, Chen, Ho, & Desmond, 2014), and its functional connections with prefrontal, parietal, and temporal cortical regions. Distributed increases to familiar stimuli in these cerebellar regions is reminiscent to activity patterns interpreted as multisensory integration in Kipping et al. (2013), and are in line with closed loop circuits of the parietal/prefrontal cortex and cerebellum lobule VI suggested by animal models (Dum & Strick, 2003; Kelly & Strick, 2003; Strick et al., 2009) and resting-state fMRI studies (Buckner, 2013; Buckner et al., 2011).

However, it is important to note that cerebellar functional activity may indicate visuomotor processes, as detailed in a review by Glickstein and colleagues (2011) implicating lobule VI as part of the "oculomotor vermis" that is active during the control of eye movements. Therefore, it is possible that activation observed in this region is not the result of familiarity, but rather of the eye movements involved. We do not have eye tracking information, but feel this concern is mitigated by our use of a comparison to examine activity (familiar > novel) so that any influence of eye movements should be the same between the two stimulus types and therefore be reduced.

Activity lobules I–IV and V is more surprising. Using intrinsic functional connectivity to examine cerebellar connections to the cortex, Kipping et al. (2013) report that lobules I–IV and V have functional connections with occipito-temporal, cingulated, and parietal regions, which they attributed to multisensory coordination of lobule I–IV. The cingulate has been implicated in remembering familiar people (Maddock et al., 2001) and familiar places (Maddock et al., 2001; Sugiura, Shah, Zilles, & Fink, 2005). Next, we looked at activity in the cerebellum specific to processing face and scene stimuli. Here, we found that the cerebellum was specific in processing faces, with activity in the I–IV, which may be driving differences observed in the overall (familiar vs. novel) analysis.

In the overall familiar versus novel contrast (faces and scenes combined), we observed differences in activity in the left inferior parietal lobule, and left middle frontal gyrus. This finding fits well with the literature, which implicates the inferior parietal lobule in judgments of familiarity (Gobbini & Haxby, 2007; Leveroni et al., 2000; Montaldi, Spencer, Roberts, & Mayes, 2006). We also observed increased activity in the left middle frontal gyrus to familiar stimuli. Activations in this area in response to familiar faces (Maddock et al., 2001; Weibert, Harris, Mitchell, Byrne, & Andrews, 2015) and scenes have been reported (Schon, Ross, Hasselmo, & Stern, 2013). It is interesting to note that cortical activations were largely observed in the left hemisphere, which has been reported to show increased activations to repeatedly presented ("learned") faces compared with novel faces (Gobbini & Haxby, 2007). The design of this study has similarities to the present study, using a method of repeated exposure to new stimuli to acquire a level of familiarity, which is then used to compare with novel stimuli. This result suggests that activity in left hemisphere cortical regions may be indicative of familiarity with stimuli, providing evidence for future assessment of hemispheric contributions to familiarity.

Again, we examined faces and scenes separately. For the familiar and novel face contrast we observed increased activity in the right posterior cingulate cortex. The posterior cingulate has been shown to be active in response to familiar face stimuli (Kosaka et al., 2003), and again has functional connections with the cerebellum, especially lobules I–IV, V, VI, and Crus I (Kipping et al., 2013). For the familiar and novel scene contrast, we observed increased activity in the bilateral precuneus. This area may reflect aspects of the task that employed processes related to episodic memory (Dörfel, Werner, Schaefer, von Kummer, & Karl, 2009) and visuospatial processing (Wenderoth, Debaere, Sunaert, & Swinnen, 2005). Functional cerebellar connections with the precuneus suggest that the cerebellum could be modulating these processes (O'Reilly et al., 2010; Zhang & Li, 2012). Activity was also observed in the middle frontal gyrus, likely driving the differences we observed in the overall familiar analysis.

Our results demonstrate increased activity in the cerebellum to familiar stimuli. This study benefits from a targeted approach to examine cerebellar responses using fMRI, including specialized sequences and processing methods. However, it is important to examine alternative explanations for the results presented. The cerebellar activity observed, especially in lobule I–IV, a sensorimotor region of the cerebellum, may be due in part to the motor response given by the participant to indicate "old" and "new" faces and scenes. We expect that by contrasting familiar and novel, both of which required a finger press, we will eliminate any influence the sensorimotor response would have. It must be considered that the activity we observed is particular to the finger used to indicate "old" (the thumb), which could artificially increase activity for familiar stimuli. Another important consideration is that the region of the vermis and bilateral I–IV are in close proximity with the border of the brain stem and fourth ventricle. We used SUIT, a high-resolution atlas template to isolate the cerebellum from the brain stem in hopes to mitigate some of this concern, but future research with high-resolution cerebellar imaging can improve our understanding of the cognitive contributions of these regions.

It is also important to point out that the cerebellar activity observed may be due to saccades (Henderson & Choi, 2015). It is possible that face processing does not require as many saccades to determine familiarity, and scene processing may require more and larger saccades to take in the entire image and determine familiarity. We feel that this concern is minor since we are not directly comparing faces with scenes, and expect that saccades to determine familiar and novel would be the same. Future research combining eye tracking would shed more light on the role of saccades in cerebellar activity during nonmotor tasks.

Another future direction for this research would be a more explicit examination of sex differences. Due to the sample of males, we were not able to compare activity between sexes. However, a significant difference in recognition accuracy between the stimulus types suggests that there may be differences in processing these stimuli. Further, prior research has revealed a dichotomy of cerebellar structure (males have larger cerebellums than females; Cho, Lee, Uhm, Kim, & Suh, 1999; Raz, Gunning-Dixon, Head, Williamson, & Acker, 2001) and function (females have greater cerebellar activity; Volkow et al., 1997) that would benefit from use of fMRI methods to provide additional understanding of how the cerebellar activity differs in these groups during familiar and novel judgments. It is possible that sex differences are underlying our results, as females have been shown to be better at face recognition (Herlitz & Loven, 2013). Due to the ratio of males to females (nearly 1:3) in our sample, any conclusions overall the participants should be made with caution, as differences observed between stimuli may be driven by the predominately female sample. Future research with a larger, balanced sample by sex is necessary to better understand the contribution of sex differences to cerebellar activity during the processing of familiar and novel stimuli.

The results of this study add to the growing list of cerebellar contributions to nonmotor functions. Here, we observed that familiar stimuli increased cerebellar activity. One way of interpreting this activity, and the cerebellar contribution to many other domains is to extend the cerebellum's role in motor behavior and learning to nonmotor activity. The cerebellum acts as a comparator, ensuring coordinated smooth movements (Brooks & Thach, 1981; Houk et al., 1993; Ito, 1984). It also acts as a key brain region in the acquisition of associative learning and implicit memories (Christian & Thompson, 2003; McCormick & Thompson, 1984; Swain & Thompson, 1993; Thompson, 1986). Rather than posit that individual processes activate discrete regions of the cerebellum, it is more likely that the cerebellum is engaged in the diffuse task of integrating multisensory input. Emerging work in animal models demonstrates that the cerebellum integrates inputs from multiple sensory modalities even at the cellular level (Huang et al., 2013; Proville et al., 2014) and there is support for this role in human cerebellar functioning as well (Kipping et al., 2013; Wiestler, McGonigle, & Diedrichsen, 2011). As a comparator, the cerebellum must be able to integrate information from multiple modalities, comparing internal states with external input, and modulating responses when necessary. It is likely that this ability extends to processes previously considered to be nonmotor, such as processing the familiarity of a stimulus. Future research specifically examining the cerebellum in various nonmotor processes is needed to understand its role as a sensorimotor integrator and the cerebellum's influence on cognition and behavior.

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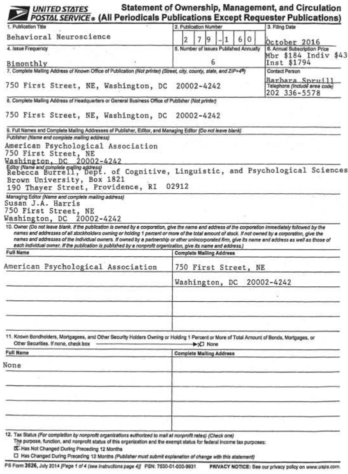

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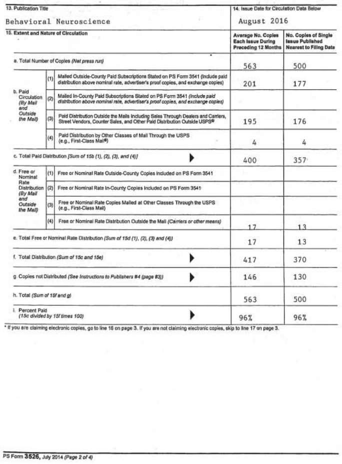

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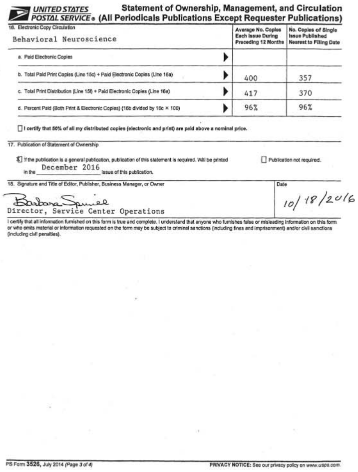

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