Investigating Causality in Brain Structures Involved in Visual Category Learning

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Abstract

Visual category learning relies not only on the ability to process sensory stimuli but also on top-down modulation that enhances task-relevant features. This study investigates functional connectivity from the Inferior Frontal Junction (IFJ) and Frontal Eye Fields (FEF) to the early visual cortex during a category learning task. Using fMRI data from 25 participants in a prior study on population tuning and visual category learning, we conducted ROI-to-ROI connectivity analyses to test whether task-related connectivity changes reflect engagement of feature-based and spatial attention systems. We hypothesize that the IFJ will show stronger connectivity with visual cortical regions during category learning, consistent with its proposed role in feature-based attention. Furthermore, we expect that this association may be more pronounced in the later blocks of the behavioral task. Our results suggest that the strongest functional coupling between frontal and occipital regions were observed for connectivity between the right IFJ and the right supracalcarine cortex, supporting the role of the IFJ in modulating visual processing. Across nearly all source–target pairs, the statistical associations with visual cortex processing became stronger during later stages of learning. These findings support theories of top-down modulation in visual learning and may have implications for neurorehabilitation strategies targeting impaired attentional control.

Introduction

Visual category learning requires the brain to distinguish incoming sensory information according to task-relevant classification rules and place them into appropriate groups. The Inferior Frontal Junction (IFJ), located at the intersection of the inferior frontal sulcus and the precentral sulcus, is a key region of the lateral prefrontal cortex (Derrfuss, Brass, Cramon, Lohmann, & Amunts, 2009). It has been identified as a hub in cognitive control networks, particularly in tasks that demand flexible attention and goal-directed behavior. Neuroimaging studies have shown that the IFJ is activated during feature-based attention, the process whereby individuals selectively attend to specific attributes– such as the color, orientation, or shape of an object– while attenuating task-irrelevant details.

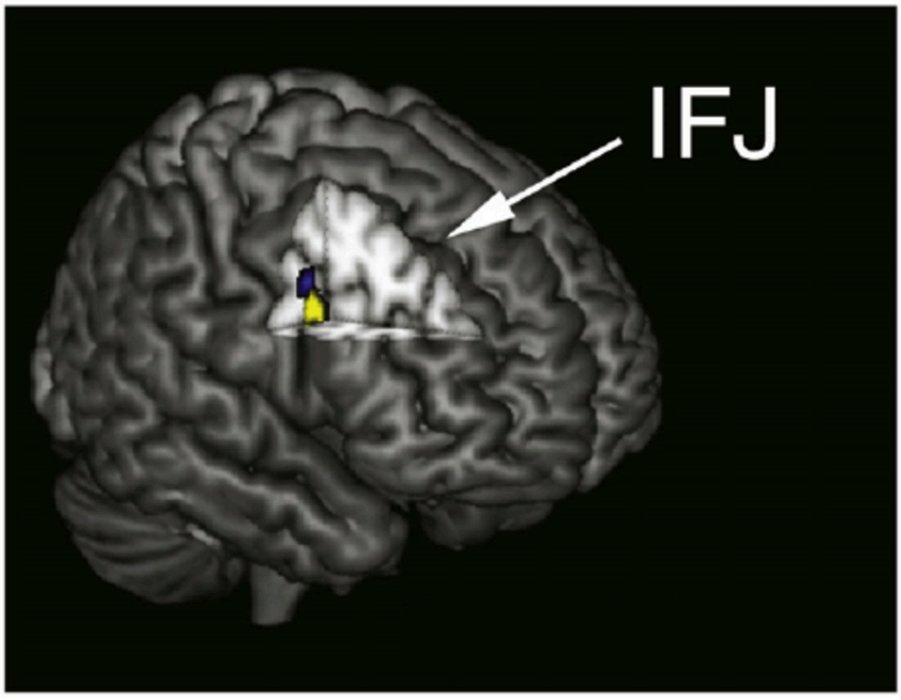

Figure 1. The Inferior Frontal Junction, a fronto-parietal region associated with top-down modulation (adapted from Zanto et al., 2010)

Top-down connectivity refers to the directional influence that higher-order cognitive regions, such as the prefrontal cortex, exert on sensory processing areas. In the context of visual category learning, this process of extracting meaningful patterns from ambiguous input is believed to be mediated by the IFJ. This dynamic interaction complements bottom-up processes, which are driven by raw sensory input from the eyes to early visual areas.

Top-down attention can be divided into feature-based and spatial mechanisms. Feature-based attention enhances processing of specific stimulus attributes– like color or orientation– across the visual field. In contrast, spatial attention selectively amplifies signals from particular regions in space, guiding perceptual resources toward relevant locations.

In addition to the IFJ, the Frontal Eye Fields (FEF) are another key top-down control region implicated in visual attention. The FEF are classically associated with the control of eye movements but are also known to influence sensory processing in posterior visual areas through spatial attention (Meyyappan, Rajan, Mangun, & Ding, 2021). Current research shows that FEF activity modulates neural responses in retinotopically organized visual cortex, even in the absence of saccades, suggesting a causal role in directing attention to specific locations. This spatially targeted modulation complements the feature-based signals associated with the IFJ, supporting a dual-system framework for attentional control during category learning. Activity in the FEF modulates neural responses in the visual cortex, enhancing processing of spatially cued stimuli even in the absence of eye movements. This modulation supports the allocation of attention to task-relevant spatial locations and is thought to operate alongside IFJ-driven feature-based control.

Although both IFJ and FEF contribute to visual attention, it remains unclear how their respective connectivity patterns relate to learning outcomes. This study investigates whether top-down signals from these regions to the visual cortex are predictive of visual processing changes during category learning. By linking connectivity patterns from the IFJ and FEF to behavioral performance, we aim to determine whether category learning can predict changes in visual processing.

Previous studies have shown that top-down modulation from the prefrontal cortex to visual areas increases as individuals acquire category rules, suggesting a dynamic role of neural networks in learning processes (Meyyappan et al., 2021). The IFJ acts as a source of feature-based attentional feedback, broadcasting signals that enhance responses to relevant features across the visual cortex, independently of spatial location (Zhang, Mlynaryk, Ahmed, Japee, & Ungerleider, 2018). The strength of these top-down connections may reflect how effectively individuals focus attention, apply internal rules, and adjust behavior to meet task demands.

In visual search and rule-guided categorization tasks, stronger IFJ-to-visual cortex connectivity has been linked to greater categorization accuracy and faster adaptation to changing rules. The IFJ also appears to coordinate with both dorsal and ventral visual pathways (Meyyappan et al., 2021), positioning it as a top-down control node that biases sensory processing in favor of task-relevant features.

Prior fMRI studies suggest that connectivity between the IFJ and visual cortex strengthens during category learning (Zhang et al., 2018). However, the relationship between these

connectivity changes and learning performance remains underexplored. Investigating whether IFJ–visual cortex connectivity predicts individual differences in visual processing could deepen our understanding of how top-down control systems shape perceptual learning.

In this study, the fMRI data we analyze from the category learning task is helpful in assessing neural tuning and changes in functional connectivity between the IFJ and visual cortex. We hypothesize that the IFJ will show increased connectivity with visual areas during the categorization task, with a more pronounced effect in later blocks of the trial. This investigation bridges behavioral learning with underlying neural mechanisms to better understand how attentional control supports flexible, goal-directed perception at the systems level.

Methods

Participants

No new participants were recruited for this study. We analyzed existing fMRI data from a previously conducted study on category learning and orientation tuning in the early visual cortex (V1–V3). The dataset includes 25 healthy adults aged 18–32 with normal or corrected-to-normal vision, though one participant's data was excluded due to excessive motion in the scanner, which led to substantial loss of visual cortex coverage (O'Bryan, Jung, Mohan, & Scolari, 2024).

fMRI Data Acquisition

Imaging was performed on a 3.0T Siemens Skyra MRI scanner at the Texas Tech Neuroimaging Institute. Structural images were acquired using a high-resolution MPRAGE sequence (TR = 2.5 s; TE = 1.7 ms; flip angle = 7°) with 172 sagittal slices at 1 mm thickness to capture whole-brain anatomy. Functional images were collected using a T2*-weighted gradient-echo EPI sequence (TR = 2 s; TE = 40 ms; flip angle = 72°; voxel size = 2 × 2 × 3 mm) across 25 axial slices (O'Bryan et al., 2024). These slices were oriented to fully cover the occipital lobe, which includes the early visual cortex and properly suited the dataset to target the top-down connectivity changes investigated in this study.

Preprocessing

After data acquisition, standard software packages (e.g. AFNI and SPM) were used for preprocessing. First, functional data underwent slice-time correction and motion-correction both

within and between scans. Slice-time correction was useful for temporally aligning different slices in a volume that were acquired at slightly different time signatures in each repetition time (TR). Then, temporal filtering at 3 Hz was performed to selectively attenuate high-frequency noise in the BOLD signal and adjust for drift, isolating the frequency range for relevant neural activity. Within-run z-scoring of voxel time series was used to correct for differences in mean signal intensity across voxels, and trial-level voxel activations were demeaned. Data were then spatially smoothed using a 4 mm full width at half maximum Gaussian kernel.

An MRI-compatible SR Research Eyelink 1000 Plus was used to ensure retinotopic locations of stimuli were consistent. Each subject completed a separate retinotopic mapping scan to acquire data on their individual early visual cortical areas (V1, V2, V3). The functional datasets were projected onto inflated cortical representations of each subject to depict the functional borders between visual areas V1v, V1d, V2v, V2d, V3v, and V3d (O'Bryan et al., 2024).

Task Design

Participants completed a visual category learning task during fMRI scanning. In each trial, they viewed a visual stimulus and were asked to categorize it into one of two groups. Feedback was provided after each response to guide learning. Importantly, participants were not given explicit instructions about the category rules and were required to learn through experience.

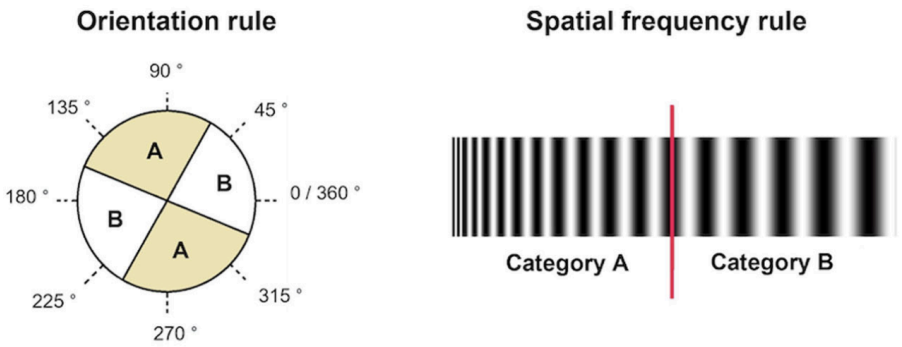

Figure 2. Two independently differing category rules of the grating stimuli that participants discriminated between in the behavioral task. (O'Bryan et al., 2024)

All of the 25 subjects whose data are represented in these findings first underwent a brief behavioral training session the week prior to scanning to familiarize themselves with the task structure and stimuli. On the day of scanning, the first scanned task which participants completed was an orthogonal contrast discrimination task intended to serve as a within-subject control. Subjects viewed the same grating stimuli but were asked to detect brief contrast changes. This design allowed controlling for stimulus exposure and visual attention without introducing categorization or involving subjects to learn categorical rules.

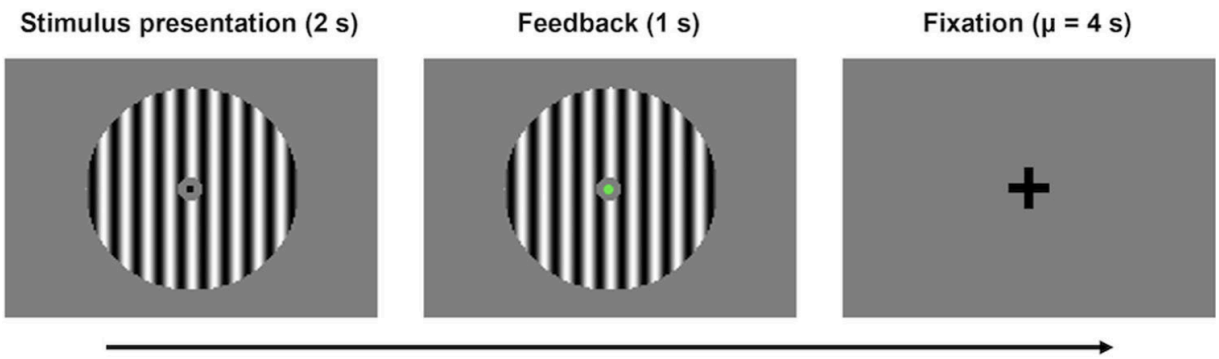

Figure 3. Stimuli and time course for an example trial of the primary categorization task with grating stimuli (O'Bryan et al., 2024)

After the behavioral training and control task, participants were split into two groups for the main categorization task. One group categorized based on orientation (n = 12), and another categorized the stimuli based on spatial frequency (n = 13). Regardless of which categorization group subjects were placed in, they all encountered an identical stimulus set over the course of the experiment. Each trial began with a 3 second grating stimulus, and both during stimulus presentation and inter-stimulus-intervals, subjects were instructed to fixate on a black marker in the screen's center. During each trial, subjects responded with a button press corresponding to their selection of either Category A or Category B, and feedback on the response's correctness was administered via a color change at the central fixation marker.

In addition to scans during the contrast discrimination and categorization tasks, all subjects separately completed a standard retinotopic mapping scan. During the retinotopic mapping scan, subjects were instructed to fixate on a rotating checkerboard and press a button when they detected a periodically appearing gray segment in the stimulus display (O'Bryan et al., 2024).

Regions of Interest (ROI)

Regions of interest (ROIs) were defined based on prior literature implicating specific prefrontal areas in top-down attentional control. Four frontal regions were selected: the left and right Inferior Frontal Junction (LIFJ: −42, 6, 30; RIFJ: 46, 12, 28) and the left and right Frontal Eye Fields (LFEF: −28, −6, 54; RFEF: 30, −6, 50). These areas were selected based on their known roles in top-down attentional control and visual processing (Bedini et al., 2023; Zhang et al., 2018). These coordinates for the IFJ and FEF were selected as established anatomical landmarks for functional activation patterns of feature-based and spatial attention, respectively (Meyyappan et al., 2021; Thompson et al., 2005).

Anatomically, the IFJ is situated at the intersection of the inferior frontal and precentral sulci (Derrfuss et al., 2009). It has been linked to rule-guided behavior and the top-down enhancement of task-relevant visual features as well as the suppression of task-irrelevant ones. The FEF is located more dorsally in the premotor cortex near the superior precentral sulcus, and while it is primarily associated with spatial attention, it has been implicated to exert modulatory influence on the visual cortex. The inclusion of bilateral IFJ and FEF regions allowed us to assess individual differences in functional connectivity with early visual cortex during category learning.

Alongside these frontal source regions, the left and right intracalcarine cortices (LICC: −10, −75, 8; RICC: 12, −74, 8) and supracalcarine cortices (LSCC: −8, −73, 15; RSCC: 8, −74, 14) were included as target regions within the visual occipital cortex to assess changes in connectivity from frontal areas during the task (Nieto-Castanon, 2023).

Connectivity Analysis

This study aimed to assess whether functional connectivity between frontal control regions and early visual cortex changes during category learning compared to a baseline control condition. Functional connectivity refers to the temporal correlation of BOLD signals between brain regions, which can reflect coordinated neural activity. In the context of category learning, such connectivity may indicate top-down modulation, where prefrontal areas bias sensory representations to enhance task-relevant visual features.

Connectivity was assessed separately for the contrast discrimination task (control) and a category learning task using identical visual stimuli. This design allowed us to isolate learning-specific changes in connectivity by holding perceptual input constant while varying cognitive demand. Functional connectivity was modeled separately for each condition, enabling direct comparison of connectivity strength across task contexts.

Identifying changes in connectivity between task conditions offers a neural signature of the cognitive processes engaged by category learning. In particular, increases in frontal-to-occipital coupling during learning would support models of top-down attentional control, suggesting that higher-order regions dynamically shape visual processing in service of rule acquisition.

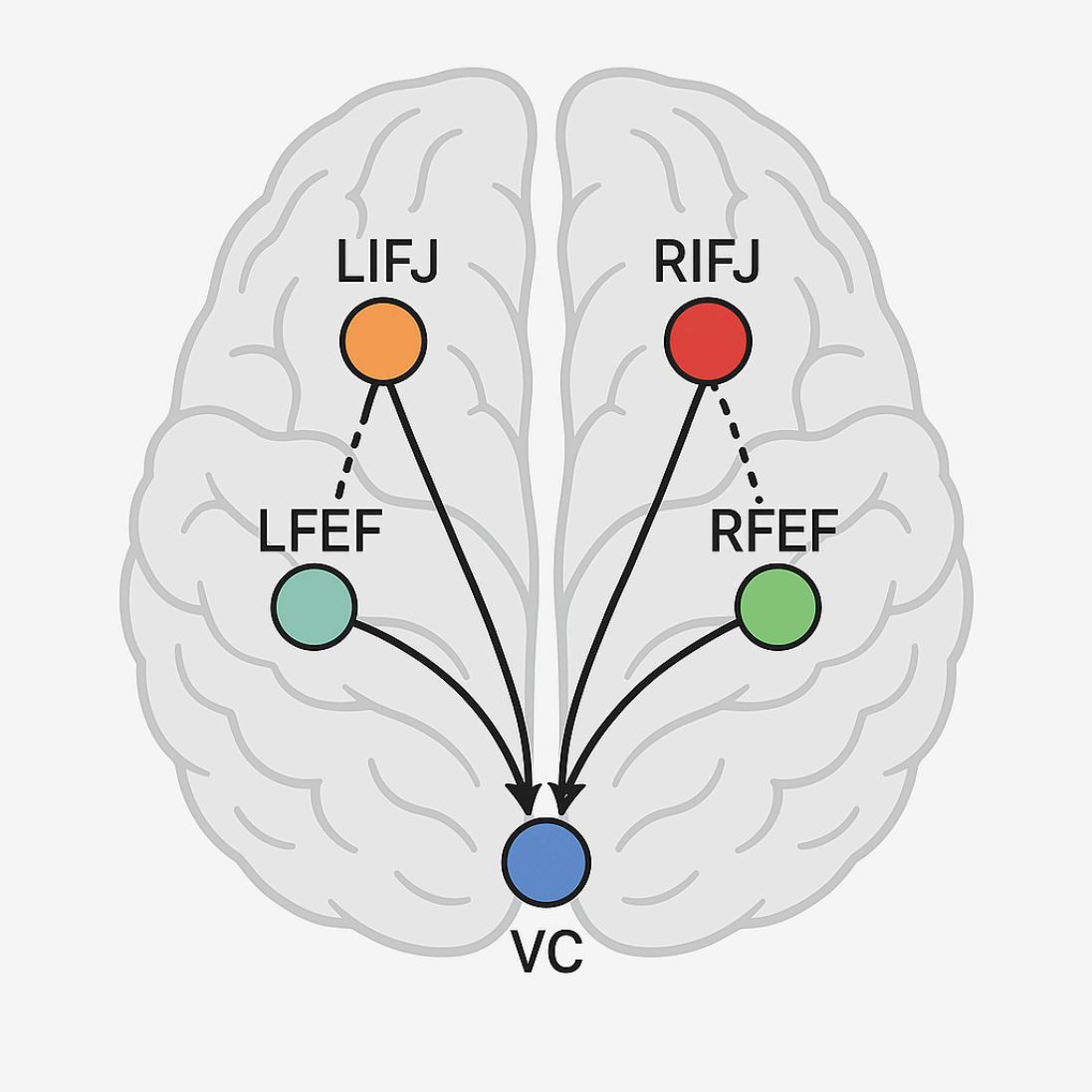

Figure 3. Schematic overview of the hypothesized top-down pathways from bilateral IFJ and FEF to early visual cortex.

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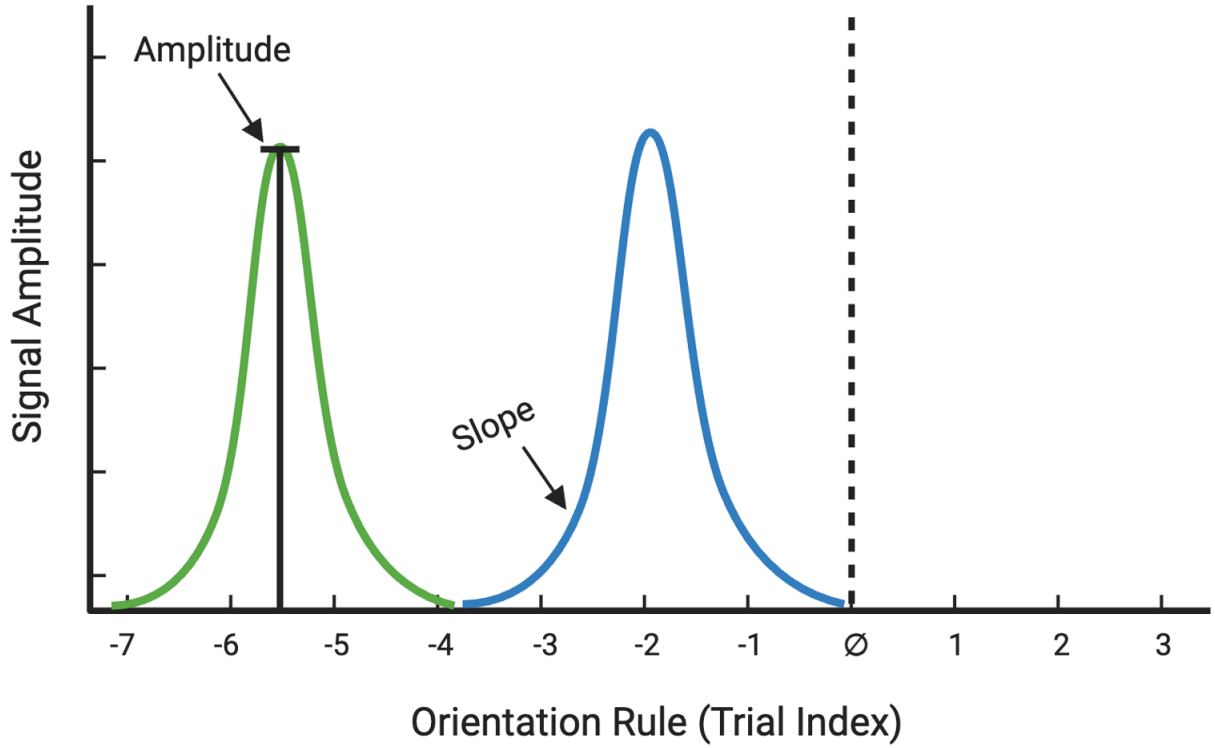

Figure 4. Modeled Neural Response Curves Illustrating Amplitude and Slope of Neural Signals

Analyses of fMRI data were performed using CONN (Whitfield-Gabrieli & Nieto-Castanon, 2012) (RRID:SCR_009550) release 22.v2407 (Nieto-Castanon & Whitfield-Gabrieli, 2022) and SPM (Penny, Friston, Ashburner, Kiebel, & Nichols, 2011) (RRID:SCR_007037) release 12.7771.

Denoising: In addition, functional data were denoised using a standard denoising pipeline (Nieto-Castanon, 2020a) including the regression of potential confounding effects characterized by white matter timeseries (5 CompCor noise components), CSF timeseries (5 CompCor noise

components), motion parameters and their first order derivatives (12 factors) (Friston, Williams, Howard, Frackowiak, & Turner, 1996), outlier scans (below 79 factors) (Power et al., 2014), session and task effects and their first order derivatives (6 factors), and linear trends (2 factors) within each functional run, followed by bandpass frequency filtering of the BOLD time-series (Hallquist, Hwang, & Luna, 2013) between 0.008 Hz and 0.09 Hz. CompCor (Behzadi et al., 2007; Chai et al., 2012) noise components within white matter and CSF were estimated by computing the average BOLD signal as well as the largest principal components orthogonal to the BOLD average, motion parameters, and outlier scans within each subject's eroded segmentation masks. From the number of noise terms included in this denoising strategy, the effective degrees of freedom of the BOLD signal after denoising were estimated to range from 430.7 to 633.4 (average 581.9) across all subjects (Nieto-Castanon, submitted).

First-level analysis RRC_REG: ROI-to-ROI connectivity (RRC) matrices were estimated characterizing the functional connectivity between each pair of regions among 9 ROIs. Functional connectivity strength was represented by bivariate regression coefficients from a weighted general linear model (Nieto-Castanon, 2020b), estimated separately for each pair of ROIs, characterizing the association between their BOLD signal time-series. Individual scans were weighted by a boxcar signal characterizing each individual task or experimental condition convolved with an SPM canonical hemodynamic response function and rectified.

Group-level analyses were performed using a General Linear Model (GLM; Nieto-Castanon, 2020c). For each individual connection a separate GLM was estimated, with first-level connectivity measures at this connection as dependent variables (one independent sample per

subject and one measurement per task or experimental condition, if applicable), and groups or other subject-level identifiers as independent variables. Connection-level hypotheses were evaluated using multivariate parametric statistics with random-effects across subjects and sample covariance estimation across multiple measurements. Inferences were performed at the level of individual networks (groups of related connections). Network-level inferences were based on nonparametric statistics from Network Based Statistics analyses (NBS; Zalesky, Fornito, & Bullmore, 2010), with 1000 residual-randomization iterations. Results were thresholded using a combination of a cluster-forming $p < 0.001$ connection-level threshold and a familywise corrected p-FDR < 0.05 network-mass threshold (Nieto-Castanon, 2020d; Benjamini & Hochberg, 1995).

General Linear Model (GLM)

The General Linear Model (GLM) is a second-level statistical framework used to assess condition-dependent effects in neuroimaging data. In this study, GLM was used to test for ROI-to-ROI connectivity changes between the contrast (control) and category learning conditions. We examined whether the correlation between group-level connectivity changes and key connectivity measures, including boundary slope, boundary amplitude, and late-phase learning measures, significantly differed from zero. This approach allowed us to isolate task-related signal changes while controlling for potential confounds and omitted variables.

Results

We first used second-level General Linear Model (GLM) results from ROI-to-ROI (RRC) analyses to assess task-related changes in functional connectivity between frontal and visual regions.

We began by examining average functional connectivity differences between the category learning and control conditions across all task blocks. This initial analysis assessed whether task-related modulation in markers of neural tuning was detectable across the entire duration of the categorization task. Using second-level GLM analyses, we evaluated associations between mean connectivity changes and markers of visual processing.

While most source–target pairs did not yield statistically significant results– with the majority of p-values exceeding 0.1– the RIFJ–RSCC connection showed a notable exception. This pair reached significance for both boundary slope ($p = 0.0177$) and boundary amplitude ($p = 0.0318$), suggesting a potential association between right IFJ connectivity and visual processing during category learning. Other connections with relatively lower p-values included LFEF–RSCC (slope: $p = 0.0644$, amplitude: $p = 0.0869$), though these did not approach conventional thresholds for significance.

Overall, while some source–target pairs showed nominal trends across all learning blocks, the overall p-values were higher and effects less robust compared to analyses focused on later blocks of learning. These preliminary results prompted a more targeted investigation of connectivity

patterns during the later stages of learning, when category representations were expected to be more fully developed.

We then focused our connectivity analysis on the later blocks of the task, as connectivity patterns were expected to be more informative once participants had acquired the category rules. For boundary slope, p-values decreased across all source–target pairs when comparing the average to the late-stage regressors, with the exception of those involving the left frontal eye field (LFEF) as the source. Similarly, boundary amplitude showed lower p-values in the later blocks for all connections except LIFJ–LSCC and RFEF–LSCC. These trends suggest that task-related connectivity shows stronger associations during the later stages of category learning.

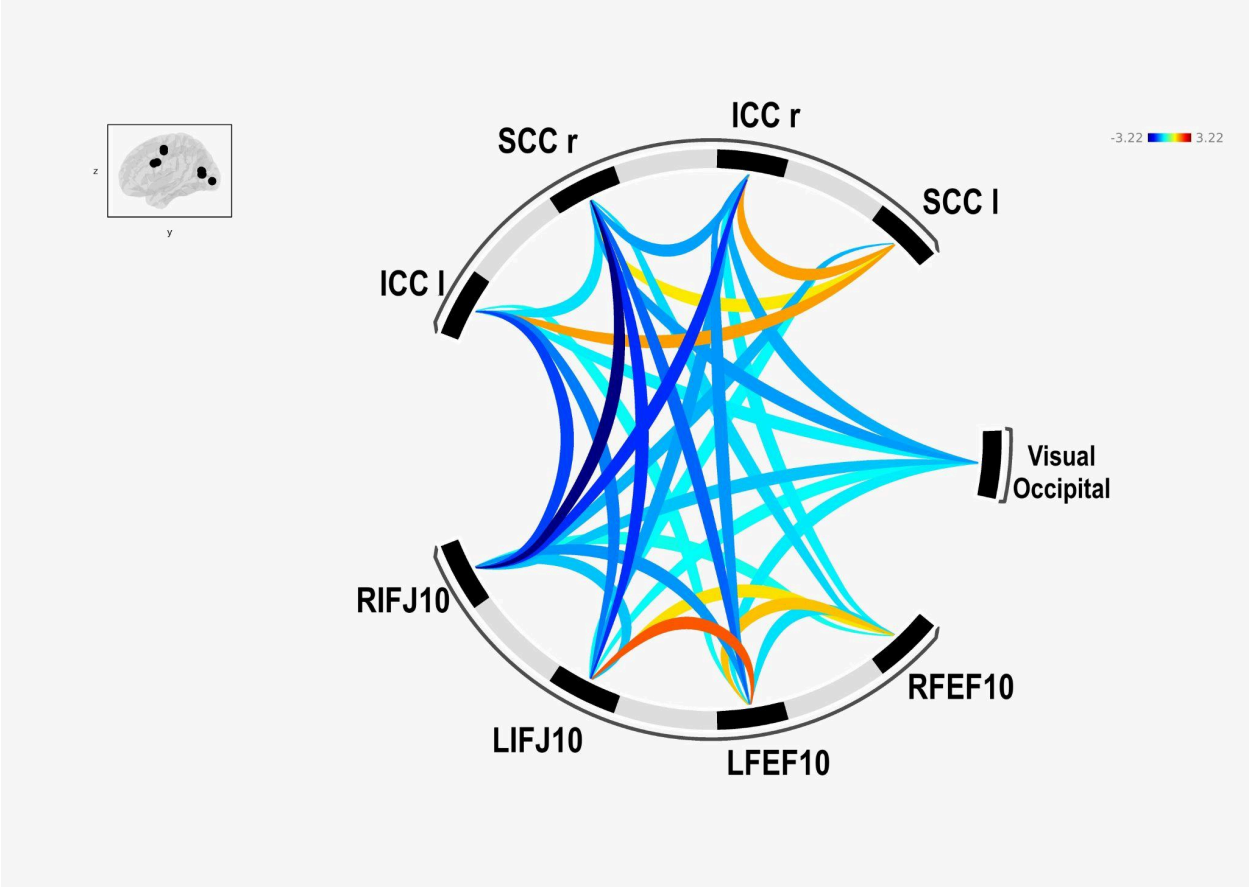

Figure 5. Connectivity differences between category learning and control conditions between frontal sources and visual cortex targets for connectivity measure *bound_slope_late* with p-values < 0.5

To investigate whether task-related changes in functional connectivity were associated with the sharpness of category learning, we performed a second-level GLM analysis of ROI-to-ROI regression using the markers for visual processing changes boundary slope (*bound_slope_late*). This regressor captures the slope of visual processing markers– where greater values may reflect more precise and marked neural tuning signatures and might indicate that participants were more consistent in classifying stimuli on either side of the boundary. Figure 5 visualizes the differences in connectivity between the category learning and control conditions, highlighting connections

between frontal control regions (IFJ and FEF) and early visual cortex (including the intracalcarine cortex [ICC] and supracalcarine cortex [SCC]). The color and thickness of each arc reflect the direction of the association, with warmer tones (yellow, orange, and red) indicating positive associations and cooler tones (blue) indicating negative associations.

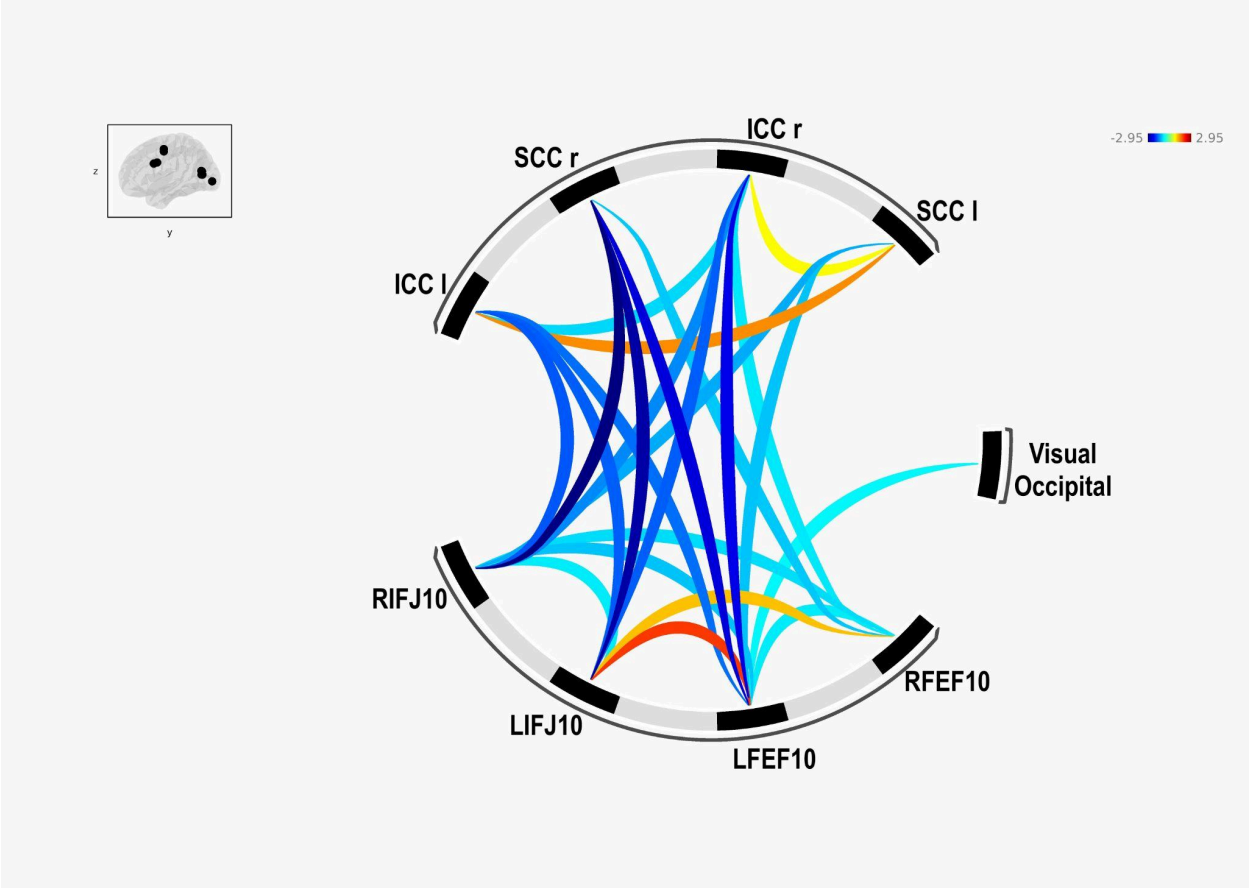

Figure 6. Connectivity differences between category learning and control conditions between frontal sources and visual cortex targets for connectivity measure *bound_amp_late* with p-values < 0.5

To complement the boundary slope analysis, we next examined whether functional connectivity varied as a function of boundary amplitude during the later stages of the category learning task.

This behavioral regressor, *bound_amp_late*, reflects the overall magnitude of differential responding across the category boundary– larger amplitudes may reflect stronger category learning, potentially indicating that participants made more decisive distinctions between stimulus classes and that signal strength increased accordingly.

Figure 6 displays the connectivity differences between the category learning and control conditions for the amplitude measure. As with the slope analysis, the visualization includes connections from frontal control regions (left and right IFJ, FEF) to early visual areas (SCC and ICC).

Source	Target	Bound Slope	Bound Amplitude	Bound Slope Late	Bound Amp Late	% Correct
LIFJ	LICC	0.275547	0.260385	0.132959	0.130359	0.445774
	RICC	0.634319	0.614431	0.361711	0.264698	0.504605
	LSCC	0.743054	0.600224	0.434632	0.653361	0.445999
	RSCC	0.226221	0.201673	0.11601	0.045471	0.41699
RIFJ	LICC	0.14837	0.208335	0.070562	0.121204	0.471234
	RICC	0.202852	0.287742	0.058098	0.188619	0.630387
	LSCC	0.297459	0.287176	0.239695	0.256551	0.387682
	RSCC	0.017728	0.031833	0.009138	0.01455	0.14188
LFEF	LICC	0.214774	0.252476	0.471427	0.148607	0.076401
	RICC	0.109927	0.189283	0.173223	0.042742	0.26962
	LSCC	0.340773	0.403709	0.562793	0.311749	0.17961
	RSCC	0.06439	0.086922	0.106314	0.036898	0.099939
RFEF	LICC	0.766269	0.891351	0.762184	0.777315	0.133425
	RICC	0.431015	0.619764	0.398011	0.414754	0.365836
	LSCC	0.897409	0.789846	0.752443	0.960765	0.540636
	RSCC	0.451078	0.514312	0.321399	0.324055	0.387395

Table 1. P-Values for Connectivity Changes Between Frontal and Occipital ROIs measured as difference in connectivity between the category learning and control task

The p-values presented in Table 1 summarize the statistical significance of ROI-to-ROI connectivity differences between the category learning and control tasks across multiple behavioral measures. Darker cells on the heatmap represent lower p-values and indicate stronger statistical evidence of a relationship, while lighter cells are reflective of higher p-values, suggesting weaker and less significant associations. Notably, connectivity between the right inferior frontal junction (RIFJ) and the right supracalcarine cortex (RSCC) exhibited some of the strongest effects across all regressors. This connection reached statistical significance ($p < 0.05$) for both boundary slope ($p = 0.017$) and boundary amplitude ($p = 0.031$).

However, the *% Correct* regressor showed null results across all connections, indicating that categorical accuracy alone may not capture the neural dynamics underlying top-down modulation.

Overall, the strongest associations were observed for connections involving the right IFJ and right SCC, with lower p-values for both slope and amplitude measures. Though other frontal–occipital pairs showed weaker and less significant associations, nearly all source–target connections showed stronger associations during the later stages of learning.

Discussion

Our results indicate that connectivity between the IFJ and early visual regions, such as the superior and inferior calcarine cortices, did not show statistically significant associations with visual processing regressors. Table 1 also shows no clear evidence of lateralization, as p-values were broadly similar across left and right hemisphere source ROIs.

In the context of recent literature on the IFJ and FEF, Table 1 suggests that task-related functional coupling between frontal and visual regions may be evident in later phases of category learning. The late-stage behavioral regressors yielded consistently lower p-values than their counterparts which were averaged across all category learning blocks, indicating stronger functional connectivity may arise once participants had learned the category rules. This may also suggest that task-related changes in connectivity between frontal and occipital regions may show stronger associations due to late-stage learning dynamics. With the exception of connections originating from the left frontal eye field (LFEF), the boundary slope late measure produced more robust effects than the average slope measure across all frontal–occipital pairs. Similarly, p-values for boundary amplitude late were lower than those for the average amplitude measure across nearly all ROI pairs, except LIFJ–LSCC and RFEF–LSCC. The weaker effects in these specific pairs may reflect individual variability in signal strength, functional overlap with adjacent regions, or a reduced role for these pathways in modulating visual cortex during late-stage learning. It is also possible that these connections are less directly involved in processing the stimulus features emphasized in this task– such as orientation or spatial frequency. Overall, the results support the hypothesis that functional connectivity becomes more behaviorally meaningful once category learning has occurred.

While prior studies suggest that top-down signals from prefrontal and parietal regions influence visual learning by biasing attention toward task-relevant features, our results did not reveal statistically significant associations between IFJ–visual cortex connectivity. The IFJ has been implicated in feature-based attention and rule-guided learning, but our findings do not provide strong evidence that its connectivity with early (e.g., calcarine) or mid-level (e.g., visual occipital) visual areas could reliably predict individual differences in markers of neural tuning or task accuracy as measured by *% Correct*.

Although our results did not reveal statistically significant associations of top-down visual cortical connectivity, the overall pattern of connectivity was consistent with a functional distinction between spatial and feature-based attention systems. Descriptive trends in the ROI-to-ROI connectivity matrix support the idea that the IFJ and FEF may differentially contribute to visual category learning, with IFJ-driven pathways more closely linked to feature-based modulation and FEF connections showing less task-related variability in this context.

These findings suggest that feature-based attention, likely mediated by the IFJ, may play a more prominent role in shaping visual cortex responses during category learning tasks that require discrimination based on stimulus features like orientation or frequency. In contrast, spatial attention mechanisms involving the FEF may be less engaged when spatial location is held constant, as in this study. Future research could clarify these roles by directly manipulating spatial and feature-based demands, helping to further delineate the distinct contributions of each system to perceptual learning.

Several limitations should be noted. While our interpretations are grounded in established anatomical and theoretical models of top-down control, causal conclusions cannot be drawn from correlational data alone. Future studies should consider employing interventional methods, such as transcranial magnetic stimulation (TMS), which may be necessary to test the causal roles of the IFJ and FEF in modulating visual processing during learning. Additionally, although our sample size was sufficient for within-subject comparisons, it may have lacked power to detect more granular individual differences or subtler interaction effects.

Another limitation involves the use of surface-based atlas ROI masks derived from meta-analyses, rather than subject-specific or volumetric masks. While surface-based approaches improve cortical alignment across participants and support within-subject analyses, they may reduce sensitivity to voxel-level variation– particularly for measures like boundary amplitude and tuning calculations. While surface-based methods improve alignment across cortical topographies and reduce inter-subject variability in cortical registration, they may introduce limitations in detecting connectivity differences that extend into subcortical or deeper cortical structures. The absence of dedicated visual cortex masks may also have reduced sensitivity to connections involving early visual areas. Finally, the task design did not orthogonally manipulate spatial and feature-based attention, making it difficult to fully identify their unique contributions.

Despite these limitations, this study advances our understanding of the neural mechanisms underlying visual category learning. By linking engagement in a category learning task that varies by orientation and spatial frequency to specific patterns of functional connectivity, we provide evidence that top-down pathways from the IFJ and other control regions play a role in

modulating sensory processing to guide learning. These findings are consistent with existing models that distinguish between feature-based and spatial attention systems, suggesting that the IFJ may play a more prominent role in modulating perception during tasks that rely on feature discrimination. This work opens new directions for research on attention-guided learning and offers a systems-level framework for interpreting individual variability in learning outcomes.

Future research could extend these findings along several paths. First, applying causal methods such as transcranial magnetic stimulation (TMS) to perturb the IFJ or FEF during learning tasks could directly test their roles in top-down modulation. Second, computational models that incorporate dynamic changes in functional connectivity may help formalize how attention systems interact with perceptual learning over time. Finally, examining these mechanisms in clinical populations with impaired top-down control (e.g., ADHD, schizophrenia) could yield valuable insights into the neural basis of attentional dysfunction and inform translational interventions.

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