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Resting-State Network Plasticity Following Category Learning Depends on Sensory Modality

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ABSTRACT

Learning new categories is fundamental to cognition, occurring in daily life through various sensory modalities. However, it is not well known how acquiring new categories can modulate the brain networks. Resting-state functional connectivity is an effective method for detecting short-term brain alterations induced by various modality-based learning experiences. Using fMRI, our study investigated the intricate link between novel category learning and brain network reorganization. Eightyfour adults participated in an object categorization experiment utilizing visual (n = 41, with 20 females and a mean age of 23.91 ± 3.11 years) or tactile (n = 43, with 21 females and a mean age of 24.57 ± 2.58 years) modalities. Resting-state networks (RSNs) were identified using independent component analysis across the group of participants, and their correlation with individual differences in object category learning across modalities was examined using dual regression. Our results reveal an increased functional connectivity of the frontoparietal network with the left superior frontal gyrus in visual category learning task and with the right superior occipital gyrus and the left middle temporal gyrus after tactile category learning. Moreover, the somatomotor network demonstrated an increased functional connectivity with the left parahippocampus exclusively after tactile category learning. These findings illuminate the neural mechanisms of novel category learning, emphasizing distinct brain networks' roles in diverse modalities. The dynamic nature of RSNs emphasizes the ongoing adaptability of the brain, which is essential for efficient novel object category learning. This research provides valuable insights into the dynamic interplay between sensory learning, brain plasticity, and network reorganization, advancing our understanding of cognitive processes across different modalities.

1 | Introduction

Learning new categories is an essential cognitive function for survival, facilitating navigation and interaction with our surroundings (Mahon and Caramazza 2009; Martin 2007; Seger and Miller 2010). New category learning is not dependent on any single neural system but rather results in requirements of various neural systems depending on the task demands (Seger and Miller 2010). These requirements make category learning as a convenient and reliable arena for studying brain mechanisms associated with cortical plasticity (Jiang et al. 2007), as it needs to combine top-down, task-specific information with bottom-up, stimulus-driven information.

Every day, we use our vision and touch senses to interact with and manipulate various objects and stimuli in our environment,

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enabling us to communicate and navigate the world around us. Remarkably, even without visual input, we can identify items by touching alone, underscoring the effectiveness of touch in object discrimination (Klatzky, Lederman, and Metzger 1985). Neuroimaging studies have revealed that both tactile and visual object categorization involve complex networks of brain regions beyond the traditional sensory cortices (Amedi et al. 2002; Kitada 2016; Lee Masson et al. 2016; Sathian 2016). When we touch an object, we initially perceive its shape, texture, softness, and temperature, processed primarily in the primary somatosensory cortex (S1) and the secondary somatosensory cortex (S2) (Kitada 2016; Sathian 2016). As we learn to categorize objects through touch, additional regions, such as the posterior parietal cortex (PPC) and the prefrontal cortex (PFC), become involved (Chapman et al. 2002; Pei and Bensmaia 2014; Sinclair and Burton 1991). Similarly, the primary visual cortex (V1) is the initial site for processing visual information, capturing fundamental features such as orientation. Visual learning enhances connectivity within the visual cortex (Bougou et al. 2024) and between the visual cortex and higher-order cognitive regions, such as the PFC and parietal cortex (DeGutis and D'Esposito 2009; Guidotti et al. 2015; Kao et al. 2020; Lewis et al. 2009). The lateral occipital cortex plays a significant role in both tactile and visual object categorization, highlighting the brain's ability to integrate sensory inputs from different sensory modalities (Amedi et al. 2002; Erdogan et al. 2016; Lee Masson et al. 2016; Lucan et al. 2010; Saito et al. 2003; Stilla and Sathian 2008). The brain's ability to adapt and reorganize its functional architecture over time shapes our capacity to learn new categories and comprehend the vast array of objects in our environment.

Resting-state functional MRI (rs-fMRI) is a powerful tool to investigate brain plasticity, which refers to the brain's ability to reorganize itself by forming new neural connections (Guerra-Carrillo, MacKey, and Bunge 2014; Kao et al. 2020) under different conditions. Unlike task-based fMRI, rs-fMRI captures the brain's spontaneous activity during rest without involving the brain in any specific task. The functional architecture of the human brain during rest comprises discrete, large-scale networks with widely spaced nodal regions, demonstrating highly correlated activity across time (Fox and Raichle 2007; Raichle et al. 2001; Vincent et al. 2007). These resting-state networks (RSNs), evident in ultra-low-frequency (<0.1 Hz) spontaneous BOLD signal fluctuations during rest, encompass mainly the default mode network (DMN) (Raichle 2015), the dorsal (DAN) and ventral attention networks (VAN) (Vossel, Geng, and Fink 2014), the frontoparietal network (Marek and Dosenbach 2018), the limbic network (Dörfel, Gärtner, and Scheffel 2020), the visual network, the somatosensory network (Damoiseaux et al. 2006), and the cerebellar network (Bernard et al. 2012). The robust correlations observed within and between these networks underscore a distinctive topography of the RSNs (Biswal et al. 1995; Fox et al. 2005; Hagmann et al. 2008). This topography aligns seamlessly with both the underlying structural connectivity of the cortex and the functional neuroanatomy of systems that collectively contribute to specific cognitive tasks and functions (Van Den Heuvel et al. 2009; Lewis et al. 2009; De Luca et al. 2005).

While numerous studies have elucidated how functional connectivity networks can be modulated by various factors, such as cognitive tasks (Fransson 2006; Schlaffke et al. 2017; Sun et al. 2007; Weisberg, Van Turennout, and Martin 2007), sensory stimulation (Hampson et al. 2004), and learning processes (Albert, Robertson, and Miall 2009; Guidotti et al. 2015; Lewis et al. 2009; Stevens, Buckner, and Schacter 2010; Vahdat, Darainy, and Ostry 2014; Waites et al. 2005), the specific effects of learning three-dimensional (3D) novel object categories through tactile and visual modalities remain unexplored. These cortical activity changes, interpreted as the plasticity of neural systems, extend beyond task-relevant networks to alterations between distinct networks (Albert, Robertson, and Miall 2009; Lewis et al. 2009; Vahdat et al. 2011; Waites et al. 2005). For instance, motor learning (Albert, Robertson, and Miall 2009; Vahdat et al. 2011) and visual perceptual learning (Guidotti et al. 2015; Lewis et al. 2009) have been shown to modify RSNs. Besides the predictive coding tasks (Barnes, Bullmore, and Suckling 2009; Lewis et al. 2009), the preparatory processes in anticipation of a task (working memory) can also influence the RSN connectivity (Jolles et al. 2013). Moreover, a recent study showed that when participants view photos of the natural or built environment, the functional connectivity of the DMN, DAN and VAN, and somatomotor networks changes (Kühn et al. 2021). The plasticity of RSNs emphasizes the dynamic role of functional connectivity in brain function to support the consolidation of previously encoded information.

Overall, the exact mechanisms by which new category acquisition influences brain networks through tactile or visual sensory modalities remain largely unclear. RSNs represent the brain's baseline activity, investigating the changes in RSNs after category learning in both tactile and visual systems is essential to understanding how the brain reorganizes itself to accommodate new information. Additionally, alterations in RSNs can serve as predictors for learning outcomes. By studying these changes, we can identify neural markers that indicate successful category learning and potentially predict future learning capabilities. Our goal is to explore how learning new object categories via tactile and visual systems can induce behavior-specific changes in connectivity within the RSNs. The main limitations of previous studies are as follows: (i) Use of two-dimensional (2D) stimuli: Most studies have utilized 2D stimuli, which differ significantly from real-life experiences (Broadbent et al. 2018; DeGutis and D'Esposito 2009; O'Bryan et al. 2024; Roark et al. 2021). (ii) Parametric shape models: Many studies have employed parametric shape models, including shell-shaped 3D objects (Lee Masson et al. 2016). However, these parametric approaches often struggle to capture the complexity of natural object shapes and may introduce confounds (Lacey and Sathian 2014). (iii) Familiar stimuli: Many studies used familiar stimuli, which can engage memory processes and influence information (Hernández-Pérez et al. 2017; Jiang et al. 2007). (iv) Lack of unified stimuli for visual and tactile learning: To the best of the authors' knowledge, no study has used similar stimuli for both visual and tactile category learning. This approach minimizes variations in stimulus features and helps capture common effects in new category learning. In the current study to overcome these limitations, we used a virtual phylogenesis (VP) algorithm to simulate the biological process and create a unique set of novel naturalistic 3D objects: the so-called digital embryos (Hauffen et al. 2012; Tabrik et al. 2021). Both the tactile and visual experiments employed identical stimuli. The digital

embryos were 3D printed for tactile testing, and we utilized virtual reality (VR) to explore 3D objects visually.

In the current study, we acquired two sets of resting-state data, pre- and post-training, to examine the learning of 3D object categories through tactile or visual modalities. Utilizing a dual regression approach, we generated subject-specific modifications of well-known RSNs. Subsequently, we conducted an in-depth statistical analysis to elucidate how learning new categories impacts RSNs and to identify potential influences of sensory modality selection on these intrinsic neural networks. Based on the literature, we expect to see enhanced functional connectivity in the FPN following category learning. The FPN is involved in cognitive control and executive functions, which are essential for processing and categorizing new information. Additionally, we anticipate increased connectivity between visual and tactile sensory networks, reflecting cross-modal integration. This integration is expected to facilitate the learning of new categories by combining information from different sensory modalities.

2 | Materials and Methods

2.1 | Participants

In this study, 84 young, healthy adults participated in two object categorization experiments. They were assigned randomly into two groups: the tactile group (n = 41, with 23 females and a mean)age of 23.91 ± 3.11 years) and the visual group (n = 43, with 21 females and a mean age of 24.57 ± 2.58 years). The Edinburgh Handedness Inventory test (laterality index ≥ 0.83) revealed that all of the participants were right-handed (Oldfield 1971). They reported no history of neurological diseases, no serious hand injuries, either healed or present, normal or corrected-tonormal vision, normal color vision, and normal hearing capacity. All participants provided informed written consent before the experiment's start and were not aware of the study's goals. The participants were compensated with €50 for their participation. All tests were authorized by the local ethics committee of the Medical Faculty at Ruhr-University Bochum (No. 17-6184). Instructions were provided only after the first resting-state data recording because knowing of the study's objectives beforehand could affect the participants' resting-state connection patterns (Guerra-Carrillo, MacKey, and Bunge 2014).

2.2 | Generation of 3D Stimuli

We generated 16 novel, naturalistic virtual 3D objects using a Virtual Phylogenesis (VP) algorithm (Brady and Kersten 2003; Hauffen et al. 2012) to create naturalistic 3D objects, also known as digital embryos. This technique ensures natural object properties and prevents the activation of memories of familiar objects that may influence perceptual processing. The VP algorithm creates a unique set of novel naturalistic 3D object categories by simulating the natural processes of morphogenesis and phylogenesis during object generation. Starting from a uniform icosahedron as an ancestor, digital embryos were created by simulating the biological processes of cell division, cell growth, and cell movement (further details are available at http://hegde.us/digital-embryos/). In the current study, we selected digital

embryos from the third generation as two different categories (eight objects per category) as depicted in Figure 1A. This algorithm allows for the independent creation of naturalistic shape variations within and across categories that are not imposed by an experimenter. It is crucial to note that, based on a pilot experiment, the overall appearance of objects within each category was similar, and distinguishing embryos between categories was not straightforward (for more information, see Tabrik et al. 2021).

2.3 | Experimental Procedure

Figure 1B provides a comprehensive summary of the experiment. Before learning the 3D object categorization using either visual or tactile sensory systems, 10min resting-state fMRI (rs-fMRI) data were recorded. In the learning phase, participants learned 16 objects from two distinct categories using either visual or tactile sensory systems. The participants attended 7 blocks, each comprising 32 trials, during which each object was presented twice. During both the visual and tactile training experiments, participants were given two optional breaks. The visual training lasted ~60min, while the tactile training lasted ~75min. After completing the learning phase, rs-fMRI data were again recorded for 10 min.

After the training sessions were completed, we administered a questionnaire to all participants to inquire about the object features they deemed important in categorizing them. The questionnaire listed seven features for participants to consider, namely: (i) weight; (ii) color; (iii) texture; (iv) global size; (v) branch size; (vi) global shape; and (vii) branch pattern.

2.4 | Visual Experiment

Participants in the visual group underwent training to visually categorize 16 objects into two categories, with eight objects per category. This was achieved through the use of VR technology in a 3D virtual environment, which was designed to simulate a real-life environment. The virtual environment, presented through an HTC Vive headset with a resolution of 1080×1200 pixels per eye (2160×1200 pixels combined) and a 110° field of view (FOV) at a 90 Hz refresh rate, included a virtual office with a desk. Participants sat on a real chair positioned in front of a virtual desk. Two perspectives of the virtual office are shown in Figure 1C. The virtual room's walls, furniture, and lighting were carefully chosen to allow the participants to easily discern the stimuli. Participants were able to freely grasp, pick up, and rotate an object using a Vive wireless controller (held in their right hand by pressing a button to hold the digital embryos) to examine it from different angles. Before starting the main task, participants were familiarized with the VR environment, the proper use of the controller, and the 3D digital embryos. First, participants were allowed 2 min to explore the virtual environment to become comfortable with the virtual workplace and limit distractions during the primary experiment. Sixteen 3D digital embryos were then placed randomly on the virtual table in front of the participants. Each participant was given up to 8s to rotate each embryo using the Vive wireless controller and become familiar with its form variations. Each trial involved



FIGURE 1 | Stimuli generation and experiment designs. (A) A "family tree" of digital embryos. An icosahedron served as the starting point for a VP process that produced 3D objects. Selected embryos reproduce in each generation Gn, resulting in generation Gn + 1. Eight G3-siblings from a single parent constituted a unique object category. Two classes of novel objects in G3 were produced by applying simulated embryonic development processes to a particular parent object from G2 (red circles). The current investigation used two object categories from the third generation as stimuli in total; the experimenter assigned numbers 1 through 8 to each category based on the siblings' corresponding positions. The subjects were not informed about the creation and/or classification process of the digital embryos. (B) A 10-min resting-state fMRI scan was the first step in the experimental design. Following that, participants completed a carefully designed training program consisting of seven blocks that were aimed at achieving particular experimental goals. A second 10-min resting-state fMRI scan was obtained on individuals after the training session to record any possible neural plasticity changes brought on by the experimental intervention. The experiments for each participant were completed in a single day. (C) In front of the participants was a furnished virtual office with a desk. There was a window to the right that provided an outside view, and to the left of the participants were bookshelves, a printer, a few books, and a monitor on a study table. (D) Visual categorization task leveraging VR technology. (E) Tactile categorization experiment using 3D tangible objects generated by a 3D printer on blindfolded participants. The objects were printed out with two different colors in order to be more recognizable for the experimenter. Since participants were unable to see the objects, this color difference did not affect the experimental results.

presenting an object at a random orientation on a virtual desk in front of the participant, who then had 4s to visually explore the object without any restrictions using the controller with their right hand. Afterward, they had to determine the object's category (category1 or category2) by pressing a left/right button on a mouse with their left hand, with no time restriction. Correct responses were indicated by a pleasant auditory signal, while incorrect responses were indicated by an unpleasant tone. The objects were presented in a pseudorandom order in fixed locations on the virtual table, as shown in Figure 1D.

2.5 | Tactile Experiment

The tactile group of participants was trained using 3D-printed versions of the same stimuli used in the visual experiment.

Throughout the experiment, participants wore eye masks to prevent the interaction of tactile and visual information. They were comfortably seated at a table with a sound-absorbing surface and allowed to explore and palpate the objects naturally using both hands, with no restrictions regarding the exploratory procedure. Similar to the visual experiment, participants had become familiar with the stimuli before the main experiment. The experimenter randomly chose a digital embryo from each of the two groups and placed it on the sound absorption plate in front of the participants. They had 12s to examine each embryo and get familiarized with its shape variations. In the main experiment, each trial began with the experimenter placing an object in a random orientation on the sound-absorbing table, after which a start signal (a beep tone of 5 kHz with 300 ms duration) played via a speaker to initiate the exploration time. After 8 s, a stop signal

(same beep tone as the start signal) was used to indicate the end of the exploration time. Since tactile exploration requires more time to perceive all features, participants were given additional time (8 s) compared to the visual experiment (4 s) to explore each object (Erdogan, Yildirim, and Jacobs 2015; Gaissert and Wallraven 2012; Tabrik et al. 2021). Participants were required to put the object back on the table. Then, they verbally categorized the object as 1 or 2, with no time restriction. Similar to the visual training session, a pleasant or unpleasant tone was used as feedback to notify participants of the correctness of their response, as shown in Figure 1E. The objects were presented in a pseudorandom order.

2.6 | Behavioral Data Processing

To determine the statistical significance of mean behavioral performance differences across blocks, we employed a repeated measures ANOVA with Greenhouse–Geisser correction to account for violations of sphericity. For both the tactile and visual groups, post hoc pairwise comparisons were performed using Bonferroni correction to control for multiple comparisons and assess the learning procedure. The questionnaire data were analyzed using two-tailed paired t tests, also with Bonferroni correction, to compare features between visual and tactile experiments.

2.7 | rs-fMRI Acquisition

Neuroimaging data were acquired utilizing a state-of-theart whole-body 3T scanner (Achieva 3T X, Philips Medical Systems, Best, The Netherlands) equipped with a 32-channel SENSE head coil, located at the Bergmannsheil Hospital in Bochum, Germany. To ensure accurate echo-planar imaging (EPI)-distortion correction, high-resolution anatomical images were obtained utilizing a whole-brain structural T1weighted MPRAGE sequence with the following specifications: repetition time (TR)=8.2 ms, echo time (TE)=3.8 ms, voxel size = $1 \times 1 \times 1$ mm³, FOV = $240 \times 240 \times 220$ mm³, and flip angle = 90°. rs-fMRI data were obtained using an EPI sequence with the following parameters: TR = 2500 ms, TE = 35 ms, flip angle=90°, 39 slices with no gap, $FOV=224\times224\times117$ mm³, and resolution = $2 \times 2 \times 3$ mm³. Each rs-fMRI scan lasted for 10 min. Participants were instructed to remain relaxed, with their eyes closed while avoiding falling asleep during the scanning process and refraining from thinking about any specific topic.

2.8 | fMRI Data Processing

All neuroimaging data were processed using tools from the FMRIB Software Library (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/ FSL, version 6.0.5.1), the Analysis of Functional NeuroImages (AFNI, version 20.0.09 https://afni.nimh.nih.gov/), Advanced Normalization Tools (ANTs, http://stnava.github.io/ANTs/), and FreeSurfer (http://surfer.nmr.mgh.harvard.edu, Harvard University, Boston, MA, USA, version 7.1.1) software. First, DICOM files were converted to NIfTI format using the dcm2niix function, and framewise displacement (FD) was calculated from derivatives of the rigid body realignment estimates to evaluate the quality of rs-fMRI data. We excluded two participants' data due to excessive head motion, where over 20% of volumes (48 volumes) were contaminated with FD > 0.3 mm. Then, motion correction was performed using FSL's motion correction tool, mcflirt function (Jenkinson et al. 2002), and slice time correction was performed for interleaved ascending acquisition with the middle slice as the reference frame. To reduce motionrelated artifacts, we applied spatial smoothing using a Gaussian filter with full width at half maximum of 6mm, using the 3dBlurInMask function of AFNI software. After removing nonbrain tissues, we applied a global intensity normalization with grand mean = 10,000 across scanning sessions for group analysis. Following the standard preprocessing steps, we used the Automatic Removal of Motion Artifacts software package (independent component analysis [ICA]-AROMA, version 0.3beta) to remove artifacts originating from in-scanner head motion. We then regressed out the mean white matter (WM), cerebrospinal fluid (CSF), and global signals from the time course of each voxel using the *fslregfilt* function. We utilized the recon-all function in FreeSurfer to remove the skull and non-brain tissue from anatomical images and segment the brain into gray matter, WM, and CSF masks. To ensure no overlap between CSF or WM masks, the masks were binarized at a threshold of 0.95. Using these masks, the voxels within each mask were averaged to create a single signal for each component. In addition, data were linearly detrended. Finally, a band-pass temporal filter (using the 3dTproject function, 0.009-0.1 Hz) was applied to the rs-fMRI data after data cleaning because ICA and confound regression can benefit from information from the full range of the frequency spectrum in separating the signal sources. The first five and last five volumes were discarded to ensure longitudinal magnetization reached a steady state and also to avoid the edge effect of temporal filtering.

To register the EPI images to the high-resolution structural (MPRAGE) images, we utilized the BBR implanted technique in FSL (Greve and Fischl 2009). We then registered the structural images to the MNI152_T1_2mm template using the Symmetric Normalization algorithm, which is a nonlinear method implanted in ANTs version 2.1.0.

2.9 | Independent Component Analyses

ICA is a computational method used to identify coherent spatial patterns in fMRI data, including RSNs and spatially structured artifacts (Beckmann et al. 2005; Beckmann and Smith 2004). In this study, ICA was carried out using FSL Melodic ICA (version 3.15) on the preprocessed data of pre-learning functional scans of both the visual and tactile groups. For dimensionality estimation of ICA, we utilized the established automatic dimensionality estimation in FSL, which employs Bayesian estimators for model order determination and applies PCA to reduce the data before IC estimation (Beckmann and Smith 2004). A group-ICA using 39 independent component maps (IC maps) was applied to detect RSNs from the pre-learning functional scans of both groups, with variance normalization used. Pre-learning scans were chosen to avoid potential biases from task-induced changes in post-learning scans, ensuring that the same RSNs were consistently used for dual regression on both pre- and post-learning

data. The estimated component maps were thresholded by dividing the maps by the standard deviation of the residual noise and then fitting a Gaussian-Gamma mixture model to the distribution of voxel intensities within spatial maps (the local falsediscovery rate at p < 0.5, (Beckmann and Smith 2004)). To select the RSNs for further analysis, FSL's "fslcc" tool was used to statistically compare each ICA component to a set of seven popular RSNs (Yeo et al. 2011). Throughout the rest of the text, whenever we refer to Yeo et al.'s networks, we will simply use the term "reference networks." The ICA components that yielded a significant correlation (Pearson's r > 0.2) with reference RSNs (Yeo et al. 2011) were selected as RSNs. P-values of correlation coefficients were calculated using a t-distribution with n - 2 degrees of freedom. Twenty-six ICA components were identified based on this procedure. Two additional ICA components were identified as cerebellar RSNs upon visual inspection. In total, 28 RSNs were entered into the dual-regression analysis. The ICA components that did not significantly correlate with reference networks were labeled as noise and excluded from further analysis.

2.10 | Dual Regression

To explore the impact of learning on the composition of the RSNs identified by the ICA, we employed a dual-regression technique implemented in FSL (Beckmann et al. 2009; Nickerson

et al. 2017). This method allows us to compare voxel-wise rsfMRI data from pre- and post-learning conditions. The dualregression process involved two steps, as shown in Figure 2. The first step, spatial regression, involved regressing unthresholded maps of the group-ICA onto each participant's functional data. Specifically, the four-dimensional (4D) rs-fMRI data were reorganized into a 2D data matrix (N voxels × T timepoints). The unthresholded group ICA components (N voxels × 28 components), which are consistent across all subjects, were then regressed into this data matrix. This process yields subject-specific time series that describe the temporal dynamics of the components (28 components×T timepoints). Each time series represents the mean signal across the voxels within the corresponding IC spatial maps. The second step of dual regression is called temporal regression. In this step, the network-specific time series (T timepoints×28 components) from previous step were used as a set of regressors in voxel-wise multiple regression analysis into the individual subject's fMRI data (T timepoints × N voxels). This step allows to identify the subjects-specific spatial maps (28 components × N voxels) that correspond to the temporal dynamics of each component. In essence, the time series that reflecting the temporal fluctuations of the group-level components were utilized to reconstruct individual spatial maps. To demonstrate the differences in both activity and spatial spread of the RSN, the dual regression analysis was carried out with variance normalization.



FIGURE 2 | The data processing pipeline for dual regression. The preprocessed rsfMRI data at MNI space were fed into the MELODIC software in FSL to run group ICA analysis. The meaningful RSNs were selected for dual regression analysis. In the first stage of dual regression, the temporal dynamics of each RSN map of each subject were extracted using a multivariate spatial regression of each spatial map into the subject's 4D space-time dataset. In the second stage, these time series were regressed into the same subject fMRI data using multivariate regression to identify the subject-specific spatial maps, one per template RSNs. FSL randomize nonparametric test was used to identify differences between groups.

To perform statistical analysis, we collected spatial maps for each original independent component across all subjects into single 4D files. To identify the differences between pre-and post-learning in visual or tactile groups (learning-specific effect) within the boundaries of the spatial maps obtained with MELODIC, we used FSL randomize nonparametric permutation testing (Jenkinson et al. 2012). This method involved 5000 permutations and a threshold-free cluster enhancement (TFCE) using a significance threshold of p < 0.05 to control for multiple comparisons (Nichols and Holmes 2002). We applied a Bonferroni correction to account for multiple comparisons across the ICs (28 components), resulting in an adjusted significance level of p < 0.0018.

To investigate the relationship between brain connectivity changes and learning progress across seven training sessions in tactile and visual category learning experiments, we used the following approach. A linear regression was fitted to performance data across sessions, with the slope serving as the learning metric. Pearson correlation was then used to calculate the relationship between parameter estimates from selected voxels (obtained through dual regression) and the learning metric. *P*values were corrected for multiple comparisons across four tests.

3 | Results

3.1 | Behavioral Data

As shown in Figure 3, performance accuracy in each block was computed for the tactile and visual groups. The statistical significance of mean behavioral performance differences between blocks was assessed using a repeated measures ANOVA with Greenhouse– Geisser correction (tactile group: F(6, 252)=40.18, p < 0.0001, visual group: (6, 228)=61.02, p < 0.0001). Behavioral performance improved significantly from the first block to later blocks, according to post hoc pairwise comparisons with Bonferroni correction for both the tactile and visual groups (p < 0.0001). Furthermore, a linear regression analysis showed a substantial increase in both groups' accuracy values (visual group: $R^2=0.917$, p=0.0007; tactile group: $R^2=0.824$, p=0.0047). Therefore, we can conclude that the results from the ANOVA indicate a significant increase in behavioral performance, and the learning criterion was reached during the respective training sessions for both groups.

The results of the questionnaire analysis revealed regardless of the sensory modality used—visual or tactile—participants in all groups consistently focused on the same aspects during category learning. However, global size was found to be a more significant determinant in the tactile experiment as opposed to the visual trial, as demonstrated by a statistically significant difference (two-tailed paired *t* test, p = 0.013, Bonferroni correction) (Figure 4). This demonstrates the complex impact of sensory modalities on the weight given to particular characteristics throughout the categorization process.

3.2 | Independent Component Analysis

The functional brain data were decomposed into 39 distinct independent spatiotemporal components using ICA. This procedure



FIGURE 3 | Behavioral performance. (A) Tactile and (B) visual experiments. The results demonstrate that participants exhibited proficient learning in categorizing both categories, irrespective of the sensory modality employed—whether visual or tactile. To further illustrate the distribution and variability in the behavioral performance data, boxplots are included for each experiment, providing a comprehensive view of the participants' performance across the two modalities.

found 28 ICA components that were significantly correlated with reference networks and 11 ICA components that were not significantly correlated with reference networks (Yeo et al. 2011). Since these 11 ICA components appeared to be artifactual signals, such as edge effects or were associated with high-frequency signals, like movement generated by a heartbeat, they were excluded from additional analysis. The 28 ICA components of interest were identified as 28 RSN components (Figure 5). Each of the 28 RSNs belonged to the cerebellar network or one of the seven major RSNs found by Yeo et al. (2011): the somatomotor network, frontoparietal network, visual network, DMN, limbic network, VAN, and DAN.

As several ICs exhibited correlations with multiple reference networks, each IC is categorized with the reference network that demonstrates the strongest correlation (Figure 5). The precentral and postcentral gyrus and paracentral gyrus (ICs 2 and 10), superior temporal gyrus and primary auditory cortex (ICs 6 and 21), and left and right postcentral gyrus (ICs 17 and 24) were the six networks that significantly overlapped with reference somatomotor network. Two cortices that correlated with reference frontoparietal network (ICs 3, 4, 20, and 26) were the dorsolateral PFC and the PPC. Subsets of the medial and superior PFC, precuneus, and posterior cingulate cortex (ICs 1, 8, and 23) are associated with reference default network.

The hippocampus and fusiform gyrus (IC 22) and the ventromedial PFC and orbital gyrus (IC 9) overlap with reference limbic network. In the cerebellar network, ICs 15 and 16 were present.



FIGURE 4 | Questionnaires for categorization tasks. Following every experiment, participants were asked to rate the importance of various features in order to determine their involvement in the tasks. Weight, color, texture, global size, branch size, global shape, and branch pattern are among the variables that are taken into consideration. With the exception of global size, which was more important in the tactile experiment than in the visual trial (two-tailed paired *t* test, *p*=0.013, Bonferroni correction), the findings show that participants concentrated on the same features in both the tactile and visual studies (two-tailed paired *t* test, *p*>0.5). The bars depicted in the figure illustrate the mean ratings across all participants for the tactile (green) and visual (red) experiments. A rating of zero signifies no importance, while a rating of six designates a feature of utmost importance. The error bars denote the standard error of the mean (SEM).

There was significant evidence of a strong correlation between reference VANs and the medial and lateral frontal cortex (ICs 11, 14, and 19). Finally, two networks overlapping with reference DAN (ICs 7 and 27) were formed of the middle frontal gyrus, inferior and superior parietal lobes, and occipital areas. Furthermore, in Figure 6, all 28 ICs from the current study are shown in different colors near reference template networks. These 28 RSN components were used as input for the dualregression technique, which was used to build subject-specific maps of the RSNs identified in the groups.

3.3 | Dual Regression Analysis

The study utilized a voxel-wise analysis with nonparametric permutation testing to identify significant test-retest changes in functional connectivity resulting from category learning, as measured by paired t tests for pre- and post-learning RSNs (using the "randomize" function from FSL with TFCE, p < 0.05). Notable results from the dual-regression analysis clarified how visual category learning affects the increase in functional connectivity in the left superior frontal gyrus within the frontoparietal network (IC 3). This effect is shown clearly in Figure 7 $(p_{\text{corrected}} < 0.05)$, where it is associated with increased coactivation in the left superior frontal gyrus. This increased coactivation in the left superior frontal gyrus illustrates changes induced by being proficient in two different categories of visual objects and emphasizes the influence of visual category learning on the frontoparietal network plasticity (r=0.37, p=0.038, Figure 9D).

In the tactile learning condition, the frontoparietal network (IC20) shows an increased functional connectivity in two discrete regions: the right superior occipital gyrus, which extends into the precuneus cortex (Figure 8B, $p_{\text{corrected}} < 0.05$), and the left middle temporal gyrus (Figure 8A, $p_{\text{corrected}} < 0.05$). Figure 9A,B illustrates the association between connectivity changes in the left middle temporal gyrus (r = 0.34, p = 0.049) and the right superior occipital gyrus (r=0.40, p=0.027), respectively, with enhanced behavioral performance during tactile category learning. Changes in functional connectives show that this expansion is closely linked to the tactile category learning effect. Simultaneously, Figure 8C $(p_{\rm corrected} < 0.05)$ shows increased functional connectivity in the subcortical somatomotor network (IC 2) in the left parahippocampus after tactile category learning which is associated with greater behavioral performance during tactile category learning (r = 0.34, p = 0.048, Figure 9C). These subtle changes highlight how tactile category learning may influence functional connectivity and provide important insights into the distributed functional changes throughout the brain in response to sensory-motor learning events. For details on the size of significant clusters identified in the dual regression analysis, please refer to Table 1.

Subsequently, the unanswered question of whether the exploratory process-that is, the sensory modalities-may have an impact on functional connectivity remains unanswered. Even though the types of objects in the tactile and visual categorization tests were identical, the question of whether the sensory modality affects functional connection was investigated. Using the second dual-regression (unpaired t test), we performed a comparative analysis between the tactile and visual groups during post-learning sessions to clarify the impact of sensory modality on functional connectivity. The findings showed that individuals who were trained in tactile categorization and those who were trained to categorize visual objects have different patterns of connectivity. Higher functional connectivity was seen in visual category learning, as shown by the increased functional connectivity of the right posterior cingulate with the visual network (IC 12), the right middle frontal gyrus with the somatomotor network (IC 10), and the right angular gyrus with the default network (IC 1) (Figure 9A). On the other hand, tactile category learning showed enhanced functional connectivity, which was represented by increased coupling between the right anterior aspect of the cerebellum and the default network (IC 23) and the left anterior aspect of the cerebellum and the cerebellar network (IC 15) (Figure 9B). These results highlight how different functional connection patterns are shaped by sensory modalities when learning visual or tactile categories.

4 | Discussion

For over 25 years, the concept of brain functional connectivity during rest has been extensively explored. This connection can be broken down into several well-known RSNs (Power et al. 2011; Yeo et al. 2011). These networks enhance our knowledge of cognition by illuminating the intricate interactions across brain networks when there are no explicit tasks or external stimuli present. Understanding the dynamics of the resting state also supports the research of many neurological and



FIGURE 5 | Selected RSNs of interest. The 28 RSNs are grouped into the cerebellar network, or seven categories based on reference networks (Yeo et al. 2011)—somatomotor, frontoparietal, visual, default, limbic, ventral, and dorsal attention networks. Each component that is significantly associated with more than one reference network is grouped with a reference whose overlap is stronger than that of other references. The threshold level is at z > 4.

psychiatric diseases by providing crucial insights into the fundamental operations of the brain (Daliri and Behroozi 2013; Lee, Smyser, and Shimony 2013). Lately, there has been a growing interest in investigating the learning-induced plasticity in resting functional connectivity under different circumstances (Albert, Robertson, and Miall 2009; Guidotti et al. 2015; Lewis et al. 2009; Schlaffke et al. 2017; Stevens, Buckner, and Schacter 2010; Vahdat et al. 2011; Vahdat, Darainy, and Ostry 2014). In the current study, we used ICA in group participants and dual regression analysis to investigate changes in RSNs following the learning of novel categories in both tactile and visual modalities. By utilizing novel 3D digital objects within a VR environment, along with 3D-printed versions of similar objects, we aimed to create a learning experience that closely mimics real-world interactions. Our results demonstrated significant changes in functional connectivity within the PFN, with increased connectivity between the FPN and the left frontal gyrus during visual

category learning, and distinct connectivity patterns emerging in the FPN following tactile category learning. This work advances our understanding of the neural mechanisms underlying category learning across sensory modalities and highlights the adaptability of RSNs in response to new learning experiences.

4.1 | 3D Environment

In this study, our focus was on investigating the plasticity induced by category learning in RSNs, utilizing both visual and tactile sensory modalities using 3D objects. To achieve this, we collected rs-fMRI data both before and following 3D shape category learning training sessions. Previous studies have demonstrated that human perception of familiar objects is influenced by higher-order cognitive functions, including memory (Amedi et al. 2002; Metzger and Drewing 2019; Norman



FIGURE 6 | Comparison of RSNs from the current study to template networks from Yeo et al.'s study. Template networks from Yeo et al.'s study are depicted in red on the left side of each group. On the right, a composite image combines all RSNs from the current study for each template network, represented in multiple colors.

et al. 2008) and prior knowledge of objects to integrate sensory systems (Ernst and Bülthoff 2004). To eliminate memory involvement during the learning process, we generated a distinct collection of novel and naturalistic 3D objects using a VP algorithm known as "digital embryos" (Hauffen et al. 2012) to simulate learning of unknown categories. One goal of this study was to eliminate the experimenter's influence and minimize tactile influences during active visual exploration to create a more realistic environment where participants may interact with the learning 3D object categories. Furthermore, neuroimaging studies have shown that cortical mechanisms for 3D shape processing differ between vision and touch, whereas the cortical mechanisms for 2D form are similar (Hsiao 2008). To address these goals, the visual experiment made use of VR technology, which allowed for active and unrestricted visual exploration in the absence of further tactile input. In the tactile experiment, individuals were blindfolded and used 3D plastic printouts to examine identical things.

4.2 | Flexibility of the FPN During Visual and Tactile Category Learning

Our results highlight the fact that category learning is not only capable of reshaping RSNs but that the particular sensory modality used in the learning process also has a unique effect on resting-state functional connectivity. The development of the right FPN toward the left SFG is associated with the learning of visual categories. On the other hand, tactile category learning is linked to the expansion of the right FPN to the left middle temporal gyrus and the right superior occipital gyrus. These findings provide compelling support for the flexible hub theory of FPN (Cole et al. 2012; Cole, Reynolds, et al. 2013; Cole, Laurent, and Stocco 2013; Miller and Cohen 2001; Zanto and Gazzaley 2013). The flexibility hub theory of FPN suggests that the human capacity to adaptively perform a wide range of tasks is primarily driven by the operation of this network. The FPN can rapidly configure its global functional connections with other brain networks based on task demands. The impact of category learning using both visual and tactile sensory modalities highlights the remarkable plasticity inherent in the FPN. This flexible reconfiguration is crucial for integrating information from various sources and coordinating appropriate responses, making the FPN a central player in goal-directed behavior and cognitive flexibility (Cole, Reynolds, et al. 2013; Zanto and Gazzaley 2013). Furthermore, the identified patterns of connectivity within the FPN play a crucial function as a code that may be transferred to facilitate the acquisition of proficiency in novel tasks. This suggests that the plasticity of FPN is a fundamental mechanism that allows the network to



FIGURE 7 | Dual-regression results depicting induced changes in the frontoparietal RSN following visual category learning. The dualregression input RSN is represented by the red-yellow color gradient, while the dual-regression outcomes are represented by the blue hue. Blue-highlighted regions correspond to individual differences in visual categorization learning and show increased connectivity around the left superior frontal lobe. Subject-specific functional connectivity parameters (PE) were plotted next to the dual-regression result. IC 3 network is correlated with reference frontoparietal network.

efficiently encode, and process information linked to various task demands.

4.3 | Visual Category Learning

Increased coupling between the right FPN and the left SFG on visual category learning task is consistent with findings showing FPN changes associated with complex cognitive processes, including categorization, working memory, attention, and episodic memory retrieval (Buzsáki and Draguhn 2004; Fox et al. 2006; Martínez et al. 2013). The role of the frontal cortex in maintaining and implementing categorization rules (Antzoulatos and Miller 2011; Freedman et al. 2001; Muhammad, Wallis, and Miller 2006) and the parietal cortex in integrating category information with motor responses (Freedman and Assad 2006; Freedman and Assad 2009; Swaminathan and Freedman 2012) are both evidence for this finding. Furthermore, our discovery is in line with Braunlich et al.'s research emphasizing the critical role of the FPN in categorization and visual feature processing (Braunlich, Gomez-Lavin, and Seger 2015). Nevertheless, the impact of left SFG lesions on cognition (Boisgueheneuc et al. 2006) and the diverse roles of the SFG associated with different networks (Li et al. 2013), suggest the SFG's contribution to higher cognitive functions. All these studies support the observed heightened connection between the FPN and the left SFG during visual

category learning as a higher cognitive function in the current investigation.

4.4 | Tactile Category Learning

The tactile category learning task revealed significant associations with variations in somatomotor RSN and FPN. Specifically, the FPN showed higher co-activation in the left MTG, right superior occipital gyrus extended to the precuneus cortex, whereas the left parahippocampus showed enhanced co-activation in the somatomotor RSN.

A recent study emphasized the crucial role of the MTG in the creative concept generation process, emphasizing its involvement in recognizing novelty features and forming new associations during novelty processing (Ren et al. 2020). Additionally, evidence indicates that the MTG is involved in the formation of new semantic associations, inhibiting the default interpretation of a task-relevant semantic notion, and searching for distinct semantic associations (Davey et al. 2016; Jung-Beeman 2005; Whitney et al. 2011). The occipital cortex exhibits remarkable adaptability by extending its functional repertoire to encompass a broader range of sensory modalities. Contrary to its historical designation as a visual center, recent research has unveiled the cortex's capacity to process diverse sensory information, such as tactile and auditory stimuli, particularly after prolonged visual deprivation (Jiao et al. 2023; Sathian 2005; Schroeder and Foxe 2005; Silva et al. 2018). The neuroplasticity observed in the occipital cortex underscores the dynamic nature of the brain, emphasizing its capacity to reorganize and optimize functionality in response to altered sensory input. The precuneus, an integral component of the DMN, has been characterized in prior research as a multisensory operator with a specialization in spatial processing (Reed, Klatzky, and Halgren 2005; Renier et al. 2009). Concurrently, the superior parietal regions play a key role in converting sensory inputs into a unified coordinate system, facilitating multimodal spatial processing (Creem and Proffitt 2001; Goodale and Milner 1992; Reed, Klatzky, and Halgren 2005; Saadon-Grosman, Arzy, and Loewenstein 2020). The FPN, on the other hand, is involved in mediating higher-order cognitive activities such as categorization and decision-making by transforming sensory information into action (Braunlich, Gomez-Lavin, and Seger 2015). Frontal areas, which are known for establishing and enforcing categorization rules, have been linked to cognitive ability (Antzoulatos and Miller 2011; Freedman et al. 2001; Muhammad, Wallis, and Miller 2006). Speculatively, the increased co-activation of the FPN in the MTG and right superior occipital gyrus extended to the precuneus cortex may arise from the formation of new memories related to tactile novel information through novel semantic associations and retrieval of acquired memory, facilitating novel object categorization.

The perceptual motion system, which is located in the pre/postcentral gyrus, is likely a key area in processing action-related information, involving mental manipulation of spatial representations of tools or objects, particularly when using the right hand (Binkofski et al. 1999; Johnson-Frey 2004; Martin et al. 1996; Rumiati et al. 2005). Furthermore, the parahippocampal



FIGURE 8 | Dual-regression analysis illustrating tactile category learning effects. The dual-regression input RSN is represented by the red-yellow color scale, while the dual-regression outputs are represented by the blue hue. The blue highlights correspond to regions where tactile category learning varies among individuals. Increased connectivity was placed (A) left middle temporal gyrus, (B) in the right superior occipital gyrus extending into the precuneus cortex, and (C) the left parahippocampus. Subject-specific functional connectivity parameters (PE) are presented alongside each dual-regression result. IC 20 and IC 2 networks were correlated with reference frontoparietal and somatomotor networks, respectively.

cortex is important for mental stimulation and prospective coding (Bellmund et al. 2016). Recent insights from Barnett et al. (2021) further, highlight a connection between the somatomotor RSN and the parahippocampal cortex. Additionally, there is strong evidence that the parahippocampal cortex is involved in tactile information processing (Pereira et al. 2007) and plays an important role in forming new concepts (Mack, Love, and Preston 2018). Our results suggest a potential link between the left parahippocampus and somatomotor RSN, indicative of its role in learning and processing tactile information, as well as mental manipulation of the spatial representation of 3Dobjects, which is essential for the complex task of categorizing novel tactile objects.



FIGURE 9 | Correlation between brain connectivity change and learning progress across different brain regions. The scatterplots illustrate the relationship between parameter estimates extracted from voxels in the (A) right superior occipital gyrus extending into the precuneus cortex, (B) left middle temporal gyrus, and (C) left parahippocampus, plotted against each participant's learning metric during the tactile category learning task. Panel (D) shows the correlation of parameter estimates from voxels in the left superior frontal lobe with each participant's learning metric during the visual category learning task. The learning metric, derived from the slope of a linear regression fitted to behavioral performance data across sessions, represents the rate of learning improvement for both visual and tactile category learning experiments.

	Center of cluster				р	Cluster size (voxels)
Task	IC	Х	Y	Z	TFCE _{corrected}	2 mm ³
Visual	3	-24	-2	63	0.038	58
Haptic	2	-24	-33	-16	0.042	43
	20	-64	-41	3	0.028	53
	20	35	-77	41	0.021	106
Visual > Haptic	1	52	-67	34	0.039	40
	10	31	22	44	0.031	55
	12	13	-50	8	0.037	73
Visual < Haptic	15	31	-44	-30	0.043	40
	23	-6	-43	-25	0.031	45

TABLE 1 | Summarized dual regression results. This table provides the center of each cluster for anatomical localization. The *p*-values of TFCE were corrected for multiple comparisons using Bonferroni correction.

5 | Impact of Sensory Modalities on Functional Connectivities

We explored whether post-learning modifications in RSN connectivities were dependent on the sensory modalities. To this end, we used the dual-regression approach (unpaired t test) to compare functional connectivity patterns between individuals who had been trained on tactile and visual category learning at post-learning sessions. The findings indicated that distinct areas of the brain were involved in visual and tactile category learning (Figure 10). In particular, increased coupling of the right posterior cingulate with the visual network is consistent with studies indicating that learning increases connectivity within relevant brain networks (Guidotti et al. 2015). This implies that the brain's spontaneous activity can represent task-relevant information even during rest. Additionally, the somatomotor



FIGURE 10 | Dual-regression results unveil the role of sensory modality in shaping functional connectivity during category learning. (A) Dual-regression analyses reveal that visual categorization leads to varying three RSNs. The right angular gyrus with IC 1, the right middle frontal gyrus with IC 10, and the right posterior cingulate gyrus and cerebellum with IC 12 demonstrated stronger activity in the visual category learning task. (B) The results also revealed that the anterior part of the cerebellum, coactivating with IC 15 and IC 23, exhibited significantly higher activity in the tactile category learning task. Subject-specific functional connectivity parameters (PE) are presented alongside each dual-regression result. ICs 1 and 23, default network; IC 10, somatomotor network; IC 12, visual network; IC 15, cerebellar network.

network's engagement may be attributed to the integration of visual and motor processes during learning since participants were required to explore 3D virtual objects using a joystick and move their hands around (Guidotti et al. 2015; Zhou and Fuster 2000). The right angular gyrus, a key node in the DMN, is known to play an important role in integrating visual information with semantic knowledge, which is crucial for visual category learning (Kuhnke et al. 2023).

The cerebellum is well-known for its involvement in motor regulation and coordination, but it also contributes significantly to sensory processing and cognitive functions (Jacobi et al. 2021). During tactile category learning, the cerebellum helps in processing and integration of tactile information, which is essential for learning new tactile categories. The cerebellum's role in tactile learning reflects its ability to facilitate sensory

discrimination and the integration of sensory inputs with motor responses (Albert, Robertson, and Miall 2009; Niu et al. 2021). The increased connection with the DMN suggests that tactile learning may engage cognitive processes linked to the integration and consolidation of new tactile information.

Our data showed massive changes in specific networks following tactile and visual learning. Similarly, huge changes in network connectivity can also be expected following acquired blindness or severe motor deficits. This will almost certainly create different baseline conditions compared to the groups of healthy individuals we studied here. Furthermore, many studies showed changes in cross-modal learning in groups of blind individuals (Park and Fine 2024; Tao et al. 2017). Therefore, our data might imply major implications for understanding category learning in people with blindness or severe motor deficits. However, further studies are needed using our particular approach to clarify the specific outcome differences in specific subgroups of individuals.

Several issues remain to be addressed in the future. Our study focused exclusively on visual and tactile modalities, which may not fully capture the effects of other sensory modalities such as auditory or olfactory. Future research should explore how these additional modalities influence category learning and restingstate changes to provide a more comprehensive understanding of sensory processing and neural adaptation. Additionally, our study did not track changes over an extended period, limiting our understanding of how neural changes evolve over time during category learning and whether these changes in RSNs can lead to sustained improvements in category learning and sensory processing in the long term. This necessitates recording brain activity during the training phase, which requires further investigation. Moreover, we only focused on unimodal learning; it would be interesting to investigate the effects of cross-modal learning on RSNs, considering that tactile and visual modalities are often used interchangeably in daily life. In terms of data processing, the BOLD signals of all sessions were filtered into the frequency range of 0.009-0.1 Hz in the current study. However, future research should consider time-scale or frequency-specific brain functional networks across sequential behavioral states to provide deeper insights into the neural mechanisms underlying category learning.

6 | Conclusions

In this study, we explored the complex dynamics of resting-state functional connectivity and its plasticity during the acquisition of novel categories in both visual and tactile sensory modalities using 3D objects. Our main goal was to bridge the gap between controlled laboratory experiments and the applicability of our findings to real-world perceptual learning. Although the 3D objects used in this study do not exist in the real world, they were intentionally designed as entirely new shapes unfamiliar to participants. This approach minimized the influence of prior experience or memory, allowing us to study category learning in a purely novel context. By examining how the brain adapts to the multidimensional nature of unfamiliar objects, we gained valuable insights into the neural mechanisms of learning. These findings add an important dimension to our understanding of the brain's adaptive processes in recognizing and categorizing objects in complex, real-world environments. The results shed light on the brain's FPN flexibility, revealing distinct connectivity patterns during visual and tactile category learning tasks. Support for the FPN's flexible hub theory emphasizes its dynamic reconfiguration in mediating higher-order cognitive tasks. This study sheds light on the intricate interplay between sensory modalities and brain networks, enriching our understanding of how the brain navigates the complexities of learning in diverse perceptual domains by providing valuable insights into the neural mechanisms underlying category learning.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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