

# Visual Category Learning Results in Rapid Changes in Brain Activation Reflecting Sensitivity to the Category Relation between Perceived Objects and to Decision Correctness

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## Abstract

■ Little is known about the time scales in which sensitivity to novel category identity may become evident in visual and executive cortices in visual category learning (VCL) tasks and the nature of such changes in brain activation. We used fMRI to investigate the processing of category information and trial-by-trial feedback information. In each VCL task, stimuli differed in three feature dimensions. In each trial, either two same-category stimuli or two different-categories stimuli were presented. The participant had to learn which feature dimension was relevant for categorization based on the feedback that followed each categorization decision. We contrasted between same-category stimuli trials and different-category trials and between correct and incorrect categorization decision trials.

In each trial, brain activation in the visual stimuli processing phase was modeled separately from activation during the later feedback processing phase. We found activation in the lateral occipital complex, indicating sensitivity to the category relation between stimuli, to be evident in VCL within only few learning trials. Specifically, greater lateral occipital complex activation was evident when same-category stimuli were presented than when different-category stimuli were presented. In the feedback processing phase, greater activation in both executive and visual cortices was evident primarily after “misdetections” of same-category stimuli. Implications regarding the contribution of different learning trials to VCL, and the respective role of key brain regions, at the onset of VCL, are discussed. ■

## INTRODUCTION

Visual category learning (VCL) is the cognitive process enabling humans to acquire, based on several experiences, a generalized and meaningful mental representation of objects. VCL involves learning which visual features are shared by objects from the same category, which features differentiate between categories, and the interdependences among those features (Filoteo, Lauritzen, & Maddox, 2010; Sloutsky, 2010; Goldstone, Lippa, & Shiffrin, 2001). When objects of interest differ in multiple salient visual features, VCL results in enhanced capacity to allocate attention to features that are most relevant for categorization, while effectively discarding irrelevant differences between objects (Hammer, 2015; Sloutsky & Fisher, 2008; Kruschke & Blair, 2000; Nosofsky & Palmeri, 1996). For example, it would take one eating no more than a few lemons to learn that lemons, unlike oranges, are sour. Such experiences would help the learning individual to avoid eating other lemons by making it possible to infer which visual features (e.g., color and shape, but not necessarily size) reliably differentiate lemons from oranges.

The nature of neurocognitive processes engaged at the onset of visual learning is largely unknown. One

possibility is that, early in the course of learning, the processing of visual information is primarily based on a bottom-up information stream, where visual cortices execute lower-level processing of visual impressions and feed the processed visual information to higher-level executive brain regions. In turn, executive brain regions use the visual information, often together with supervisory information (e.g., feedback, reward, category labels, or equivalent constraints; Hammer, 2015), to infer and learn the categorization rule. Only at later learning stages, after the categorization rule has been learned and consolidated (Vogel, Woodman, & Luck, 2006), might category-related changes in object representation become evident in visual cortices. A second possibility is that the kind of information encoded in visual cortices during VCL differs from one learning trial to the next, so as to reflect specific and immediate task requirements. In such a scenario, changes in representation reflecting category-related information might become evident in visual cortices within very few learning trials. This may indicate modulation of stimuli representation in a very short time scale, associated with top-down attention processes that may facilitate learning (Hochstein & Ahissar, 2002). Such top-down effects on visual cortices may be evident as sensitivity to the categorical relation between perceived stimuli, sensitivity to decision correctness after the introduction of supervisory information,

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(such as feedback), or both. Currently, there are no direct evidences to support either one of these alternatives.

Earlier studies, however, did show extensive VCL resulting in lasting changes in neural representation, indicating sensitivity to the learned visual categories, primarily in the lateral occipital complex (LOC), a visual processing brain region known to be most sensitive to object-like stimuli (Brants, Bulthé, Daniels, Wagemans, & de Beeck, 2016; Cheadle & Zeki, 2014; Davis & Poldrack, 2014; van der Linden, Wegman, & Fernández, 2014; Folstein, Palmeri, & Gauthier, 2013; McGugin, Gatenby, Gore, & Gauthier, 2012; Gureckis, James, & Nosofsky, 2011; Jiang et al., 2007; Kourtzi & Kanwisher, 2001). Others showed that patterns of activation in the LOC, when categorizing familiar objects, depend on context and task-related goals (Harel, Kravitz, & Baker, 2014), indicating category-specific top-down modulation in visual cortices.

Here, we tested if changes in brain activation, associated with the learning of novel object categories, may become evident within a few learning trials. In the tested VCL tasks, differences between stimuli (between categories and within categories) were fairly salient. Thus, learning did not necessitate the acquisition of perceptual expertise (unlike, e.g., Folstein et al., 2013 or Jiang et al., 2007), and instead, it primarily involved inference and attentional learning (Sloutsky & Fisher, 2008; Kruschke & Blair, 2000). Learning in such tasks was found to be fairly rapid, much faster than in scenarios where learning requires acquisition of perceptual expertise (Hammer, Klout, & Booth, in press; Hammer, Sloutsky, & Grill-Spector, 2012, 2015).

We compared LOC activation with patterns of activation in lateral prefrontal executive cortices known to be involved in VCL (specifically the middle frontal gyrus [MFG]). The MFG contributes to VCL by taking part in critical basic cognitive processes to include volitional attention control, working memory, and inference (Swaminathan & Freedman, 2012; Ashby & Maddox, 2011; Cromer, Roy, Buschman, & Miller, 2011; Wolfensteller & von Cramon, 2011; Seger & Miller, 2010). The novel design enabled testing how the categorical relation between perceived visual stimuli interacts with feedback information (associated with the participant's decision correctness) and how this interaction is reflected in patterns of activation in the LOC, in comparison with activation in key executive cortices.

## METHODS

### Overview

Each participant performed multiple short VCL tasks, each with a distinct stimulus set. In each set, stimuli differed in three binary feature dimensions. In each VCL task, the participant's goal was to learn how stimuli differ and which feature dimension was relevant for categorization based on trial-by-trial feedback. In each trial, two "creature-like" stimuli were presented successively. The

participant had to decide if the two creatures were from the same category or from different categories. After each categorization decision, the participant received feedback indicating decision correctness. Trials were modeled into four types: (i) hits, trials in which the participant correctly identified two creatures as belonging to the same category; (ii) correct rejections (CRs), trials in which the participant correctly identified two creatures as belonging to different categories; (iii) misses, trials in which the participant incorrectly identified two creatures as belonging to different categories; (iv) false alarms (FAs), trials in which the participant incorrectly identified two creatures as belonging to the same category. This enabled contrasting between same-category trials and different-categories trials (category relation contrast) and between correct categorization decisions and incorrect decisions (decision correctness contrast) and investigating the interaction between the categorical relation between perceived stimuli and the participant decision correctness. Activation during the stimuli processing phase was modeled separately from activation during the feedback processing phase (see Lopez-Paniagua & Seger, 2011, for a similar analysis approach).

### Participants

Sixteen right-handed adults, with normal or corrected-to-normal vision and no history of neural or psychiatric disorders, performed the experiment. One participant was excluded from the analysis because of extensive head movements, and another was excluded because of chance-level performance in most of the VCL tasks. The remaining 14 participants included nine women, and their mean age was 25.1 years ( $SD = 1.9$  years). This is a sufficient sample size given the within-participant design and the objectives of the current study—characterizing basic brain function in a fairly homogeneous population (Friston, 2012; Friston, Holmes, & Worsley, 1999). Participants gave informed written consent in accordance with a protocol approved by the Stanford University institutional review board. Each participant received \$60 for participation.

### Materials

Each participant completed 12 VCL tasks and six active baseline (BL) tasks in a single fMRI scanning session. Each task was based on a distinct stimulus set. A stimulus set that was used in a VCL task by some participants was used in a BL task by other participants. That is, stimulus sets were counterbalanced across participants and VCL/BL tasks. Participants were familiarized with the experimental procedure by performing four VCL and two BL tasks 1–2 days before the scanning session and again during the structural MRI scans that took place at the beginning of the scanning session. The stimulus sets used for training were not used in the primary experimental tasks.

In each task, a distinct stimulus set of novel “alien creatures” was used (see examples in Figure 1 and Appendix A). Each stimulus set included eight monochromatic creature-like stimuli that differed in three salient binary feature dimensions. In each VCL task, the participant had to learn which feature dimension was relevant for categorizing the stimuli into two distinct “alien subspecies” and to ignore irrelevant feature dimensions. The three feature dimensions by which stimuli varied were similarly salient, and thus, it was unlikely to infer the relevant feature dimension based on visual saliency. Saliency assessments were based on pilot testing and were further validated based on participants’ performances in the BL tasks (see also Hammer, Sloutsky, et al., 2015; Hammer et al., 2012).

For the functional localizer scan, which took place at the end of the scanning session and was used to identify brain regions sensitive to complex visual stimuli (i.e., the LOC), we used grayscale renderings of the stimuli and phase-scrambled renderings of these grayscale images (see Appendix A). The phase-scrambled images preserved low-level characteristics of the creatures’ images while eliminating characteristics of a coherent object. This allowed localizing object-sensitive visual cortices (LOC) of each participant and dissociating these from lower-level visual cortices.

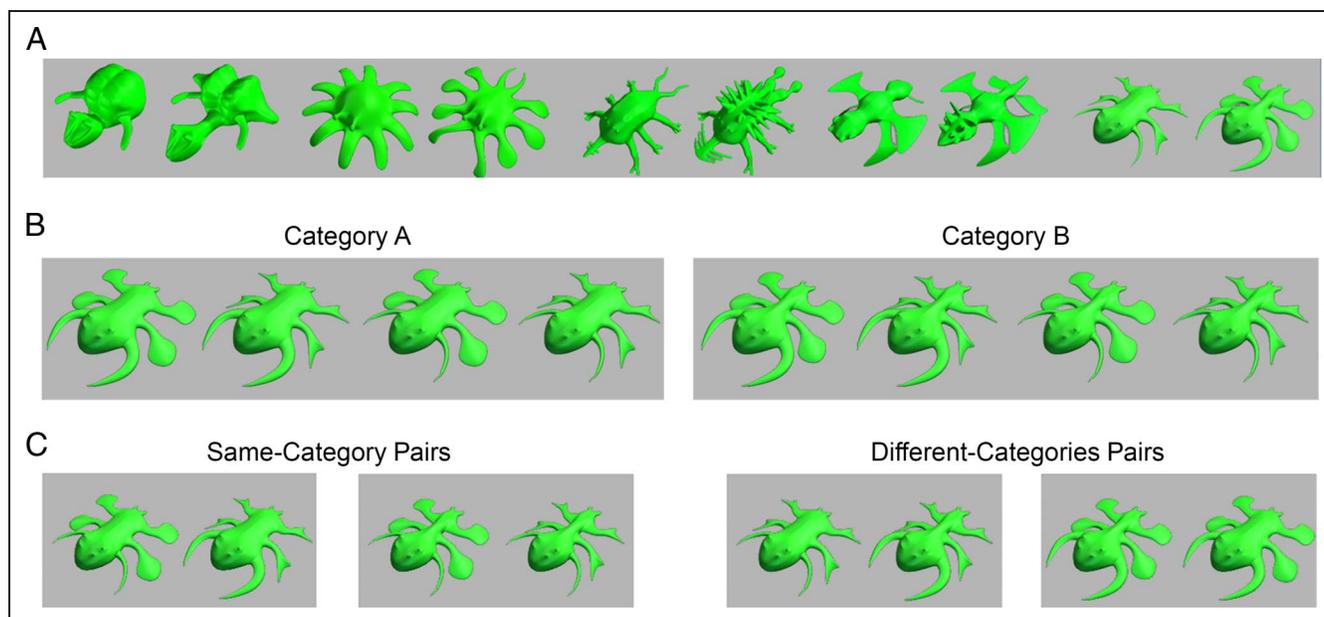
Psychtoolbox (MATLAB; The MathWorks, Natick, MA) running on a MacBook computer was used for stimuli presentation and participants’ response recording. In the scanning session, stimuli were presented at the center of a 30-in. 2560 × 1600 pixels computer display placed on the back of the scanner bore, which was reflected on a mirror

mounted on the fMRI scanner head coil. Stimuli occupied between 10° and 12° of the participant’s field of view.

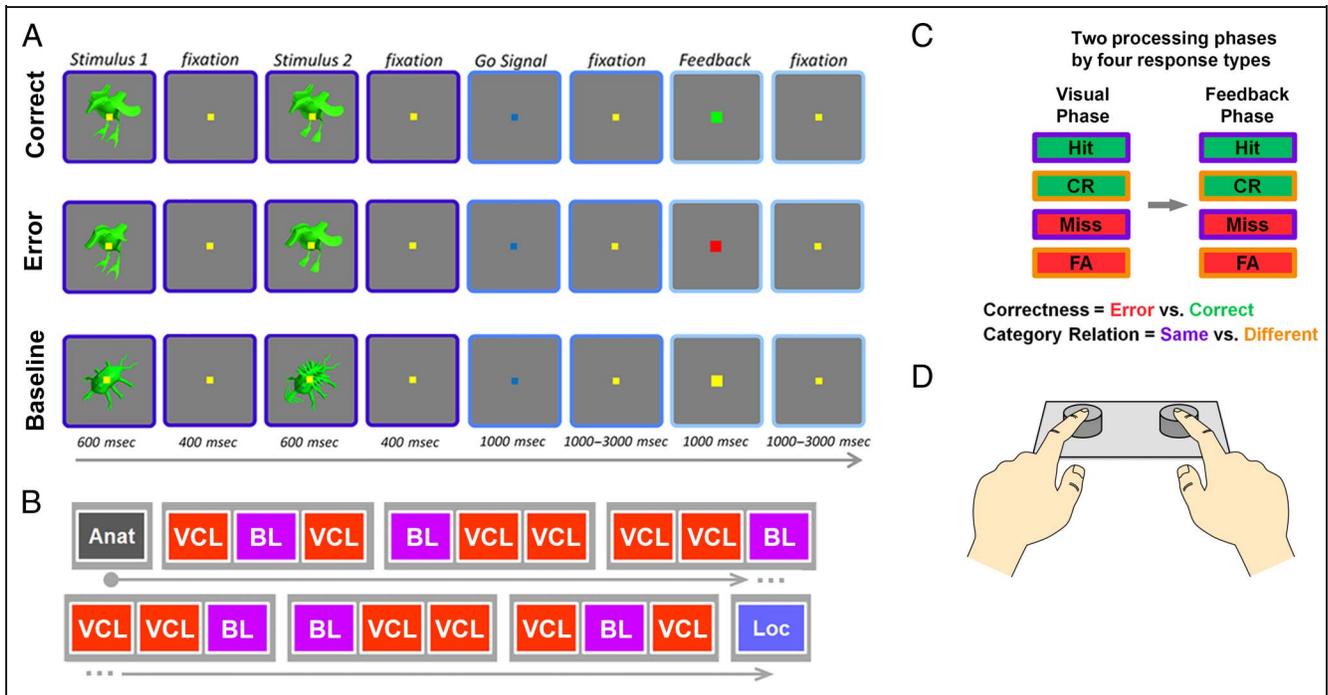
### Category Learning Tasks and BL Tasks

In the 12 VCL tasks, the participants received trial-by-trial feedback (the yellow fixation point was replaced by a small green square after a correct decision or red square after an incorrect decision). In the six BL tasks, there was no informative feedback (the yellow fixation point was replaced by a small yellow square after an on-time response, regardless to the response correctness). In the BL tasks, participants were instructed to make their best guess regarding which feature dimension was relevant for categorization and to categorize the stimuli based on this feature dimension. This required participants to pay attention to the stimuli and to execute keypress responses similar to what they did in the VCL tasks.

Although in the BL tasks, participants could not, and were not expected to, infer the predetermine categorization rule (at least not better than chance level, on average), we separated BL trials into hits, CRs, misses, and FAs based on the scheme used in the VCL tasks. For example, the leftmost stimuli pair in Figure 1C was a same-category pair. When a participant pressed the right key after being presented with this pair in a VCL task, this trial counted as a hit. When a participant pressed the left key, this trial counted as a miss (the rightmost stimuli pair in Figure 1C was associated with FAs and CRs, respectively). Because of the counterbalancing of stimulus sets between participants and VCL/BL tasks, some participants



**Figure 1.** Stimuli examples (see also Appendix A). (A) Stimuli examples from five representative stimulus sets. Each set is represented by two orthogonal stimuli that differ in the three binary feature dimensions. (B) All stimuli from one stimulus set. On the left are members of Category A (broad-body creatures), and on the right are members of Category B (narrow-body creatures). Members of each category differed in their limbs and horns (irrelevant feature dimensions). (C) Across trials, same-category stimuli and different-categories stimuli (two examples of each) were matched in the number of feature-wise similarities.



**Figure 2.** Design schematics. (A) In each trial, two stimuli were sequentially presented. After the stimuli offset, the participant had to execute her categorization decision within the 1000-msec response interval signified by a blue fixation point. In VCL tasks, a green square indicated a correct decision, and a red square indicated an incorrect/error decision. In BL tasks, a yellow square indicated an on-time response. (B) Each scanning session started with two to three short anatomical scans (Anat), followed by six functional scans, each with two VCL tasks with feedback and one BL task. The scanning session was concluded with a functional localizer scan (Loc). (C) Eight event types were used for the primary analysis. These included hits, CRs, misses, and FAs, in the stimuli processing phase and in the feedback processing phase. (D) Participants used their left index finger for different-categories decisions and their right index finger for same-category decisions.

were presented with this stimulus set, and this exact stimuli pairing, in a BL task. When a participant pressed the right key after being presented with this stimuli pair in a BL task, this trial was used as a baseline for VCL hits, and when a participant pressed the left key, it was used as BL for VCL misses. That is, each BL trial had the same visual input and required similar visual-motor associations as the respective VCL trial. This enabled to better dissociate brain activation related to the inference and learning of the categorization rule based on trial-by-trial feedback, from activation related to objective characteristic of specific visual inputs, or response biases. Alternative approaches, such as averaging all BL trials together, could have introduced greater irrelevant and undesired variability to the baseline (i.e., contrasting VCL hit trials with an average BL activation based on both left-key presses and right-key presses and larger number of stimuli pairing compositions to include stimuli pairs that were not presented to any participant in VCL hit trials).

In the VCL tasks, learning and improving from one trial to the next required inference, because in each trial stimuli pairing was unique, and thus, participants could not improve performance by memorizing specific stimuli pairs presented in earlier trials.

Each task was 16 trials long, where each trial had four components: (i) visual stimuli processing phase, where the participant was presented with two stimuli one after the

other, each for a duration of 600 msec with a 400-msec fixation-only interval after the presentation of each stimulus (total = 2000 msec). During the stimuli presentation, the participants could not execute their categorization decision; (ii) 2000 msec after the trial onset, the yellow fixation point changed color to blue for a duration of 1000 msec, during which the participant had to press the right key (using the right index finger) indicating that she thought the two stimuli were from the same category, or the left key (left index finger) indicating that she thought the two stimuli were from different categories. (iii) After the response interval, there was a 1000- to 3000-msec fixation-only interval. This within-trial temporal jittering allowed dissociating neural activity related to stimuli processing from neural activity related to feedback processing. (iv) After the fixation-only interval, the participant was presented with the feedback (either green or red square in VCL tasks) or with the on-time key press indicator (yellow square in BL tasks) for a duration of 1000 msec. Feedback presentation was followed by a 1000- to 3000-msec fixation-only presentation, after which the next trial started (see Figure 2A).

The average feature-wise perceptual similarity in same-category trials matched the average similarity in different-categories trials (see Figure 1). In each task, the absolute pairwise correlations between the three feature dimensions in which the stimuli varied were minimized. That

is, if a participant were consistent in categorizing the stimuli based on one feature, her response pattern would have been significantly different from the expected response pattern if she categorized the stimuli based on one of the two other feature dimensions.

Participants used their right index finger for pressing the right key (“same-category” decision) and their left index finger for pressing the left key (“different-categories” decision). This made it easier to assess neural activity associated with the execution of motor responses (see Results).

### Functional Localizer Tasks

The localizer scan included eight blocks of creature stimuli alternating with eight blocks of phase-scrambled stimuli. In each block, a mixture of stimuli from different stimulus sets was used (see Appendix A). Each block included 16 trials, and it was 32 sec long. In each trial, the participant had to press the right key if two successive stimuli were identical and the left key if they were different.

### Scanning Session Procedure

The scanning session started with short anatomical scans (each 265 sec long), during which the participant performed some of the familiarization tasks. The use of a few distinct short scans allowed using only the better quality anatomical brain images. The anatomical scans were followed by six VCL/BL fMRI scans, each with two VCL tasks and one BL task. Within each scan, order of the VCL and BL tasks was counterbalanced. Each scan started and ended with 8 sec of fixation only. The three tasks within each scan were separated by 8-sec fixation intervals. The overall duration of each VCL/BL scan was 392 sec. The localizer scan concluded the scanning session. The duration of the localizer scan was 312 sec. The overall duration of a scanning session was 110–130 min (see Figure 2B).

### Neuroimaging Data Acquisition

Participants were scanned in a General Electric 3-T (Discovery MR750) scanner at the Center for Cognitive and Neurobiological Imaging (CNI) at the Stanford University Psychology Department, using a 32-channel head coil (Nova Medical, Inc., Wilmington, MA). For each participant, we acquired two to three whole-brain T1-weighted anatomical scans (high-resolution 3-D fast spoiled gradient recall; 160 sagittal slices, 0.938 mm × 0.938 mm, 1.000-mm slice thickness, 256 × 256 image matrix, field of view = 240 mm, flip angle = 12°). Each anatomical scan was 265 sec long. The images acquired in the anatomical scans were rendered into a single high-quality anatomical image. Gradient echo localizer images were acquired to determine the scanner field of view and the placement of the functional slices. Functional images were acquired

using a T2-sensitive gradient echo spiral pulse across 36 transverse slices covering the entire brain (repetition time = 2000 msec, echo time = 30 msec, flip angle = 77°, field of view = 224 mm, 3.2 mm × 3.2 mm in-plane resolution, 4.0-mm slice thickness, 0.0-mm slice spacing). Applying the same slice thickness, we acquired anatomical T1-weighted in-plane images that were used to co-register each participant functional datum to her whole-brain anatomical image.

### Functional Data Preprocessing

Image preprocessing and data analysis were performed using mrVista2, a MATLAB-based neuroimaging data analysis toolbox. Functional data preprocessing involved (i) slice timing; (ii) motion correction and realignment of all functional images within each scan to the eighth image within the scan, using an affine transformation (Nestares & Heeger, 2000); (iii) realignment of the seven functional scans (six VCL task scans and one localizer scan) based on each scan mean activation map; (iv) coregistration of the functional and anatomical images, for each participant individually, using her anatomical T1-weighted in-plane images; (v) applying a high-pass filter with a cutoff of 40 sec; (vi) converting the time series data to percent signal change by dividing the time series of each voxel by its mean intensity; and (vii) using standard general linear model analysis to create voxel-by-voxel activation maps. Functional data images were not spatially smoothed (see below details about the procedure used for excluding noisy voxels).

In the VCL/BL scans, beta values in each voxel were modeled based on the 26 distinct event types: two conditions (VCL vs. BL tasks), by four possible response types (hits, CRs, misses, and FAs), by three processing phases within each trial (stimuli processing, motor response execution, and feedback processing). In addition to these 24 event types, we modeled separately the fixation-only events from all trials (used for first-level baseline activation contrast) and trials in which the participant did not respond on time (these trials were excluded from later analysis). We computed the beta coefficients from a general linear model applied to the preprocessed time series of each voxel. As predictors, we used the distinct modeled experimental events convolved with the hemodynamic impulse response function used in SPM.

In the functional localizer tasks, beta values were computed for three distinct event types (using a condition/block-based predictor): blocks with creature stimuli, blocks with phase-scrambled stimuli, and fixation-only events.

### ROIs

A functional localizer (contrasting between blocked trials with creature stimuli and blocked trials with the

corresponding phase-scrambled stimuli) was used for localizing the LOC (Folstein et al., 2013). Statistically significant voxel clusters, with at least 100 functional voxels each, were found in the left and right LOCs of all participants. Significance was determined using voxel threshold of  $p < .001$ . The AFNI 3dClustSim function was used for determining significance at the cluster level (using a Monte Carlo simulation). For the MFG, the placing of sphere-shaped anatomical ROIs was done for each individual participant by mapping Talairach coordinates on the participant anatomical brain image, using the compute Talairach mrVista2 tool. Anatomical ROIs were with a radius of 15 mm (see Appendix B).

Within each ROI, voxels with low signal-to-noise ratio were excluded. Signal-to-noise ratio was calculated as the explained variance in neural activity, across all 26 modeled event types, and thus, it was not biased toward any of the later analyzed contrasts (Riggall & Postle, 2012; Kriegeskorte, Goebel, & Bandettini, 2006). In the LOCs, voxels with explained variance  $<20\%$  were excluded. In the MFGs, voxels with explained variance  $<10\%$  were excluded. Mean beta values for each ROI were calculated based on the remaining voxels.

### Behavioral Measures

We assessed overall participants' categorization accuracy using the nonparametric accuracy measure  $A'$  (Grier, 1971), which is based on the participants' hit rate and FA rate.  $A' = 0.5$  indicates chance-level performance, and  $A' = 1.0$  indicates perfect performance.  $A'$  scores close to 0.0 indicate high category sensitivity but with consistent response reversing.

Hit rate and FA rate are defined as

$$H = \text{Hitrate} = \frac{\text{Hits}}{\text{Hits} + \text{Misses}} \quad \text{FA} = \text{FalseAlarm rate} = \frac{\text{False Alarms}}{\text{False Alarms} + \text{Correct Rejections}}$$

$A'$  is defined as

$$A' = 0.5 + \text{sign}(H-FA) \times \frac{(H-FA)^2 + |H-FA|}{4 \times \max(H, FA) - 4 \times H \times FA}$$

As with the brain imaging data, we also assessed VCL performances based on the number of hits, CRs, misses, and FAs separately. In Appendix C, we assess VCL performances by accounting to possible a priori response biases, contrasting VCL with BL performances.

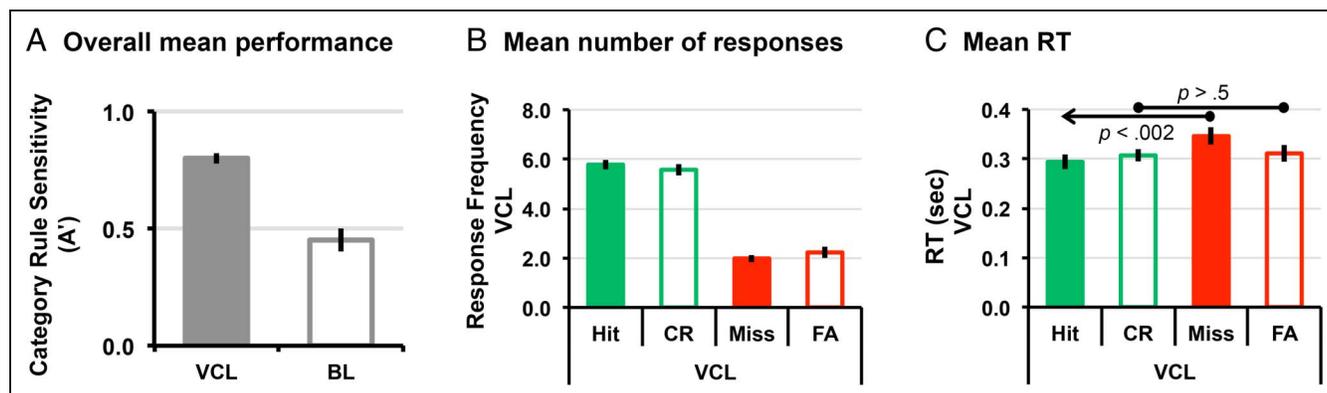
## RESULTS

### Behavioral Results

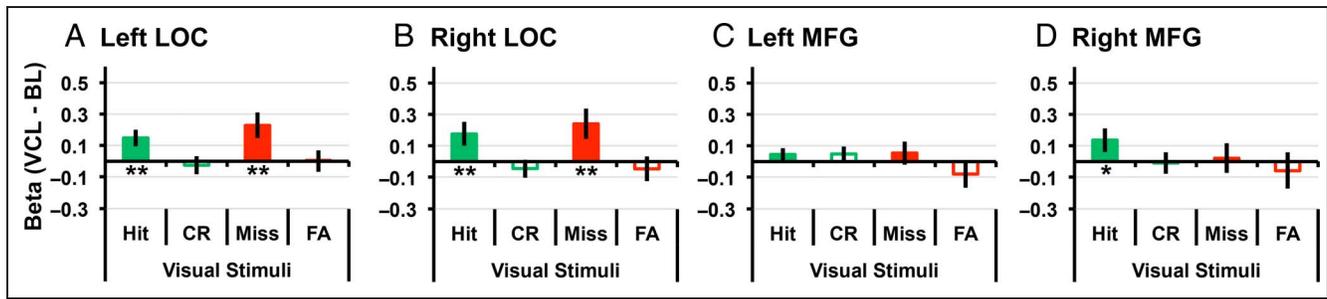
One-sample  $t$  tests (Bonferroni corrected for two tests) show that the inference of the categorization rule in the VCL tasks (mean  $A'$  score = 0.80,  $SD = 0.09$ ) was significantly better than chance ( $A' = 0.5$ ),  $t(13) = 13.03$ ,  $p < .0001$ ,  $d = 7.23$ , whereas in the BL tasks (mean = 0.45,  $SD = 0.19$ ), it was at chance level,  $t(13) = -0.98$  (Figure 3A). Paired-sampled  $t$  test shows that the mean accuracy in the VCL tasks was significantly higher than that in the BL tasks,  $t(13) = 6.46$ ,  $p < .001$ .

An ANOVA with Category relation (same/different) and Correctness (error/correct) as independent variables and VCL performances as a dependent measure resulted in a nonsignificant interaction,  $F(1, 13) = 1.32$ ,  $p > .2$ , yet in a Correctness main effect,  $F(1, 13) = 108.12$ ,  $p < .0001$ ,  $\eta_p^2 = 0.89$  (Figure 3B). This indicates that the mean number of categorization errors, in both error types (FAs and misses), was significantly lower than the number of the two types of correct categorization decisions (hits and CRs).

An ANOVA with Category relation (same/different) and Correctness (error/correct) as independent variables and VCL RT as a dependent measure shows a significant interaction,  $F(1, 13) = 4.87$ ,  $p < .05$ ,  $\eta_p^2 = 0.27$ , and a Correctness main effect,  $F(1, 13) = 23.32$ ,  $p < .0001$ ,



**Figure 3.** Mean performances in the VCL tasks. Error bars are *SEMs*. (A) Mean overall category rule sensitivity in VCL and BL tasks ( $A' = 1.0$  indicates perfect performance, whereas  $A' = 0.5$  indicates chance level). (B) Mean number of responses for each response type, per task (16 trials per task; time-off trials are excluded from the count). (C) Mean RT for each response type (see Appendix C for additional analysis).



**Figure 4.** Mean activation level (as the difference in beta values between VCL and BL tasks), in each ROI, in the visual stimuli processing phase. Error bars are *SEMs*. Significant differences (and trends) between VCL and BL, indicating sensitivity to category information, are marked as follows: \* indicating  $<.1$  and \*\* indicating  $<.05$  (two tailed; uncorrected for multiple tests). Corresponding full factorial analyses are reported in Table 1.

$\eta_p^2 = 0.64$  (Figure 3C). Post hoc  $t$  tests show significantly shorter RT for hits than for misses,  $t(13) = 4.11$ ,  $p < .002$ , but without significant differences between CRs and FAs,  $t(13) = 0.38$ . One-sample post hoc  $t$  tests show that, in the VCL tasks, only hits (correct detection of same-category stimuli) were as fast as responses in the BL tasks (VCL – BL  $\approx 0$ ). All the other VCL responses were slower than the respective BL responses, all  $ps < .05$  (see Appendix C).

#### Activation Patterns in the Stimuli Processing Phase

An ANOVA with ROIs (left and right LOCs and MFGs) and Response type (hits, CRs, misses, and FAs) as independent variables and the VCL – BL activation in the stimuli processing phase as a dependent measure shows a trend toward an ROI  $\times$  Response type interaction,  $F(9, 117) = 1.76$ ,  $p = .083$ ,  $\eta_p^2 = 0.12$ . Factorial analyses for each ROI, in the visual stimuli processing phase, show that this trend is driven by a significant sensitivity to categorical relation between paired stimuli in the left and right LOCs, but not in the MFGs. This was evident as higher levels of neural activity to same-category stimuli than to different-

categories stimuli. There was no significant sensitivity to decision correctness in the visual stimuli processing phase, in any ROI (see Figure 4 and Table 1 for the full factorial analysis).

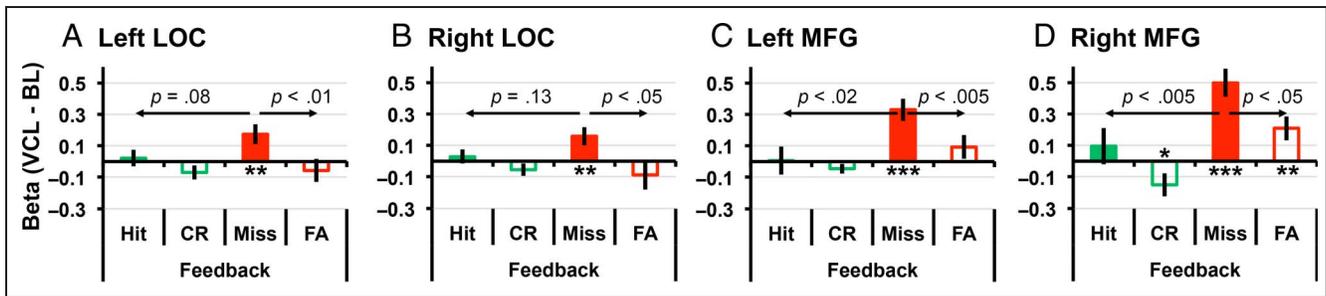
#### Activation Patterns in the Feedback Processing Phase

An ANOVA with ROIs (left and right LOCs and MFGs) and Response type (hits, CRs, misses, and FAs) as independent variables and the VCL – BL activation in the feedback processing phase as a dependent measure shows a significant ROI  $\times$  Response type interaction,  $F(9, 117) = 3.05$ ,  $p < .005$ ,  $\eta_p^2 = 0.19$ , a significant ROI main effect,  $F(3, 39) = 7.10$ ,  $p < .001$ ,  $\eta_p^2 = 0.35$ , and a significant Response type main effect,  $F(3, 39) = 8.58$ ,  $p < .001$ ,  $\eta_p^2 = 0.40$ . Factorial analyses for each ROI, in the feedback processing phase, show significant sensitivity to the categorical relation between the paired stimuli in all four ROIs, evident as higher levels of neural activity to same-category stimuli, as compared with different-categories stimuli. Significant sensitivity to categorization decision correctness was evident in the left and right

**Table 1.** Factorial Analysis for Each ROI in the Stimuli Processing Phase (VCL – BL)

	<i>L-LOC</i>	<i>R-LOC</i>	<i>L-MFG</i>	<i>R-MFG</i>
Correctness (error vs. correct)	$F = 0.72$ <i>ns</i>	$F = 0.30$ <i>ns</i>	$F = 0.56$ <i>ns</i>	$F = 0.91$ <i>ns</i>
Category relation (same vs. different)	$F = 6.52$ $p < .03$ $\eta_p^2 = 0.33$	$F = 4.98$ $p < .05$ $\eta_p^2 = 0.28$	$F = 0.75$ <i>ns</i>	$F = 1.03$ <i>ns</i>
Correctness $\times$ Category relation Interaction	$F = 0.16$ <i>ns</i>	$F = 0.20$ <i>ns</i>	$F = 2.00$ $p = .18$	$F = 0.17$ <i>ns</i>

Error trials are based on misses and FAs, correct trials are based on hits and CRs, same-category trials are based on hits and misses, and different-categories trials are based on CRs and FAs. *ns* indicates statistically nonsignificant effects, with  $p \geq .2$  (see Appendix D for similar report with the contrast VCL, fixation only).



**Figure 5.** Mean activation level (difference in beta values between VCL and BL tasks), in each ROI, in the feedback processing phase. Error bars are *SEMs*. Significant differences (or trends) between VCL and BL, indicating sensitivity to category information, are marked as follows: \* indicating  $<.1$ , \*\* indicating  $<.05$ , and \*\*\* indicating  $<.005$  (two tailed; uncorrected for multiple tests). Corresponding full factorial analyses are reported in Table 2.

MFGs (see Figure 5 and Table 2 for the full factorial analysis). Notably, both correctness and categorical relation main effects were primarily driven by greater activation associated with miss detection of same-category stimuli (misses) in VCL tasks (see Figure 5 for the relevant simple main effects).

#### Between-ROI Similarities in Activation Patterns

Similarities in activation patterns between the four ROIs were assessed using principal component analyses (PCAs) based on the VCL – BL brain activation from the four ROIs, all participants, and the four response types (standardization was based on data from all ROIs). These PCAs provide a simplified presentation of the pairwise similarities between ROIs, complementing the reported factorial analyses above. The first PCA is based on activation in the stimuli processing phase, the second is based on activation in the feedback processing phase, and the third is based on activation in the stimuli processing and feedback processing phases combined (data for each ROI were a 112-long vector = 14 participants ×

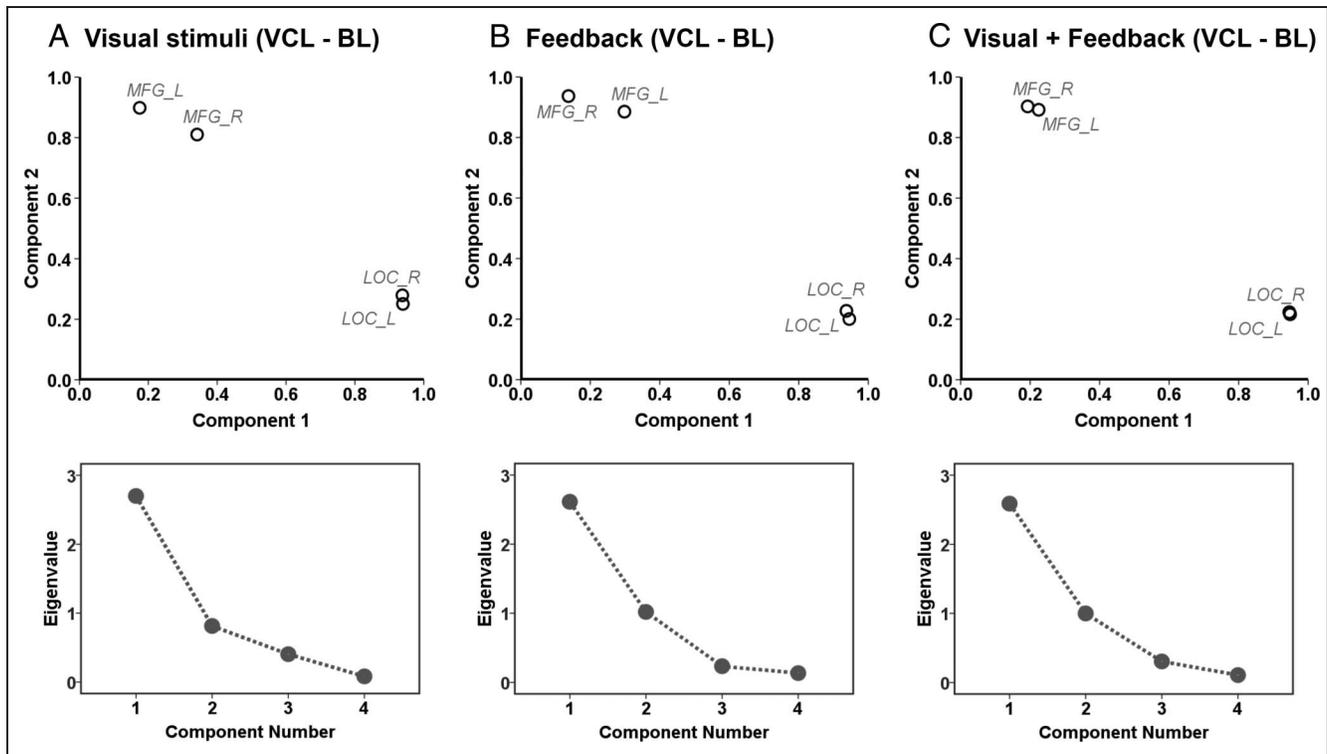
4 response types × 2 processing phases). All PCAs show that each left-hemisphere ROI did not differ much from the respective right-hemisphere ROI, whereas the LOCs differ from the MFGs in both processing phases. In all PCAs, the first two PCs jointly explained at least 85% of the variance in brain activation in the four ROIs, where each of the first two PCs (in rotated space) explained at least 40% of the variance. Each of the remaining two PCs had marginal contribution, explaining at most only 10% of the variance. The PCs plots in Figure 6 are for the orthogonal rotated PCs, calculated using varimax rotation.

The PCAs show that the pairwise response pattern of activation in the left and right LOCs was highly similar, where both ROIs had very high loadings ( $>.8$ ; loadings values range between  $\text{min} = 0$  and  $\text{max} = 1$ ) on PC-1 and low loadings ( $<.3$ ) on PC-2. In contrast, the left and right MFGs had low loadings on PC-1 ( $<.4$ ) but very high loadings ( $>.8$ ) on PC-2. That is, PC-1 primarily reflects visual perception processes, and PC-2 primarily reflects executive processes. The same pattern is largely preserved when computing the PCs based on brain activation during the stimuli processing phase (Figure 6A),

**Table 2.** Factorial Analysis for Each ROI in the Feedback Processing Phase (VCL – BL)

	<i>L-LOC</i>	<i>R-LOC</i>	<i>L-MFG</i>	<i>R-MFG</i>
Correctness (error vs. correct)	$F = 1.74$	$F = 0.67$	$F = 7.15$	$F = 17.19$
	<i>ns</i>	<i>ns</i>	$p < .02$	$p < .002$
			$\eta_p^2 = 0.35$	$\eta_p^2 = 0.57$
Category relation (same vs. different)	$F = 11.02$	$F = 8.13$	$F = 5.06$	$F = 7.30$
	$p < .007$	$p < .02$	$p < .05$	$p < .02$
	$\eta_p^2 = 0.46$	$\eta_p^2 = 0.38$	$\eta_p^2 = 0.28$	$\eta_p^2 = 0.36$
Correctness × Category relation Interaction	$F = 1.45$	$F = 1.50$	$F = 2.46$	$F = 0.07$
	<i>ns</i>	<i>ns</i>	$p = .14$	<i>ns</i>

Error trials are based on misses and FAs, correct trials are based on hits and CRs, same-category trials are based on hits and misses, and different-category trials are based on CRs and FAs. *ns* indicates statistically nonsignificant effects, with  $p \geq .2$  (see Appendix D for similar report with the contrast VCL, fixation only).



**Figure 6.** PCAs. Top shows the components plots in the rotated space, for the first two PCs. Bottom shows the corresponding scree plots. (A) PCA based on the visual stimuli processing phase. (B) PCA based on the feedback processing phase. (C) PCA based on both the visual stimuli processing and feedback processing phases.

feedback processing phase (Figure 6B), or the two processing phases combined (Figure 6C).

## DISCUSSION

This is the first study to examine the nature of immediate changes in neural activation in VCL. The novel experimental design enabled testing how category relation between objects interacts with decision correctness and how this interaction is reflected in brain activation. We found changes in representation in visual cortices (LOC), indicating sensitivity to the category relation between novel stimuli, to manifest as soon as a categorization rule was inferred. In the LOC, we found greater activation when participants were presented with same-category stimuli pairs than when they were presented with different-categories pairs. This was also evident as significantly higher activation in VCL tasks than in BL tasks only in same-category trials (Figure 4, Table 1). In the feedback processing phase, we found greater activation to same-category stimuli evident in both visual and executive cortices (MFG). In the feedback processing phase, activation primarily associated with misses (miss detection of same-category stimuli) was greater in the VCL tasks than in the BL tasks. The exception was the right MFG where FAs were also associated with greater activation in VCL than in BL. VCL – BL activation associated with misses was greater than the activation asso-

ciated with the other response types, in all four ROIs (Figure 5, Table 2).

The short duration of each VCL task makes it most likely that the category-related activation evident in visual cortices was associated with top-down attention, rather than being reflective of category sensitivity taking place autonomously within visual cortices. Learning to allocate more attention to the task-relevant feature dimension might have resulted in distinct buildup of feature-related neural activation during the presentation of two same-category stimuli (identical in the relevant feature dimension). When different-categories stimuli (differed in the task-relevant feature dimension) were presented, there was no such activation buildup, thus the lower BOLD response. Because of the short stimuli presentation, and given that the second stimulus in a trial could have not been predicted from the first stimulus, activation buildup from one stimulus to the next is likely to be observed—more likely than feature-related adaptation because of neuronal fatigue or stimulus expectation (Larsson & Smith, 2012).

In the feedback processing phase, higher activation after miss detection of same-category stimuli might have resulted from executive brain regions reactivating visual cortices to access residual representation of recently perceived stimuli (Hochstein & Ahissar, 2002; Harrison & Tong, 2009), enabling learning after unexpected decision errors. This might have resulted from a bias were participants

relied more on same-category stimuli processing than on different-categories stimuli processing, a bias also evident in the behavioral findings. Specifically, the RT for hits in the VCL tasks was as short as the RT in the BL tasks. In contrast, RT for misses was longest. RT for correct and incorrect detection of different-categories stimuli was at intermediate level, without significant differences between the two (Figure 3C). These may indicate highest confidence when correctly detecting same-category stimuli, contrasted with lowest confidence when “miss detecting” same-category stimuli. This may suggest that participants were paying more attention to same-category trials than to different-categories trials, which in turn may indicate greater contribution of same-category trials to VCL. Preference toward same-category comparison in VCL has been reported before. It was suggested that such a preference results from same-category comparison being, on average, more informative for learning than between-categories comparison, at least in everyday-life VCL scenarios with salient between-category differences (for related discussions, see Carvalho & Goldstone, 2015; Palmeri & Mack, 2015; Hammer, Brechmann, Ohl, Weinshall, & Hochstein, 2010; Hsu & Griffiths, 2010; Hammer, Diesendruck, Weinshall, & Hochstein, 2009; Hammer, Hertz, Hochstein, & Weinshall, 2007, 2009; Hammer, Bar-Hillel, Hertz, Weinshall, & Hochstein, 2008; Erickson, Chin-Parker, & Ross, 2005; Kareev & Avrahami, 1995).

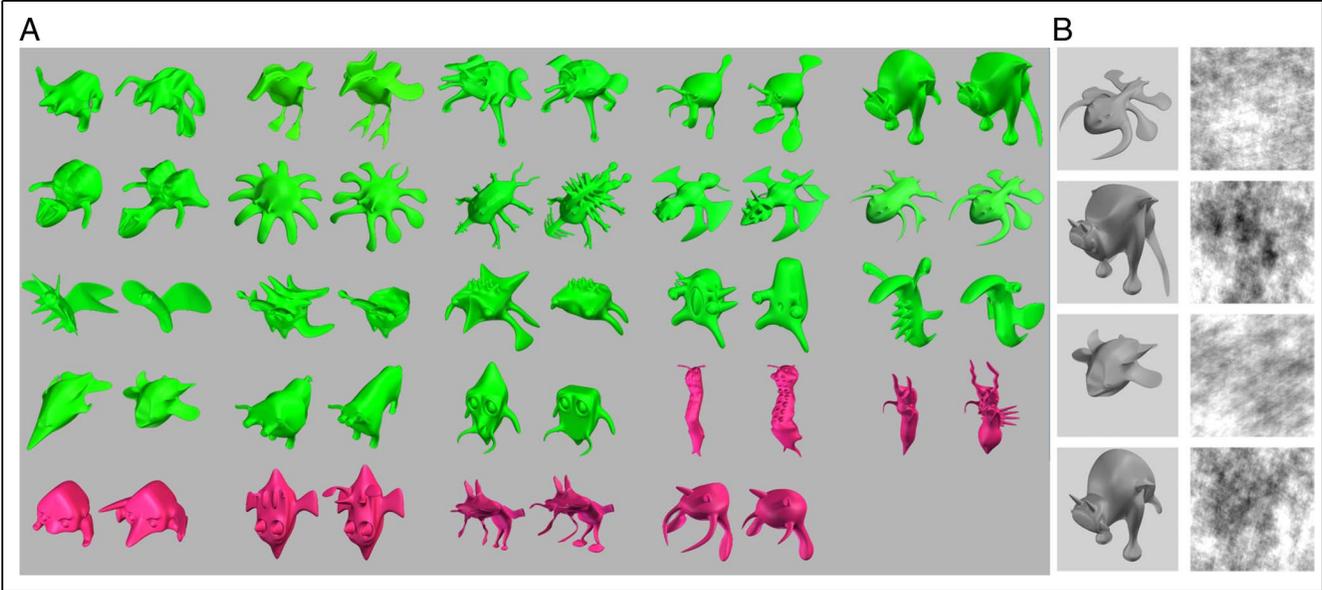
Sensitivity to the categorical relation between stimuli in the LOC was evident starting at the stimuli presentation phase, before the execution of the categorization decision, and regardless to its correctness. It is simple to acknowledge that hits reflect the participant’s capacity identifying paired stimuli as members of the same category and thus being associated with distinct activation. However, having similarly greater activation in the stimuli processing phase associated with misses seems baffling at first—if a participant recognized two stimuli as members of the same category (as might be suggested by the level of activation, matching hits), why did she make a categorization error? This behavior/activation pattern might be explained by the fact that the number of misses in each VCL task was small (about 2, on average; a total of about 24 misses per participant in all 12 VCL tasks), where some misses may have occurred after the participant likely inferred which feature dimension was task relevant (note that the frequencies of misses and FAs were similar; see

Appendix 3). It is possible that many of the categorization errors were associated with a mild uncertainty, or response confusion because of haste, and not because of the participant being fully unaware of the categorization rule (see Braunlich & Seger, 2016, and Paul et al., 2015, for related findings, and Trapp & Bar, 2015, for a related discussion).

In the feedback processing phase, greater activation in same-category trials was evident in all ROIs. In the MFGs, we also found significant sensitivity to the decision correctness (error > correct). These may reflect neuro-cognitive processes involved in working memory, attention control, and inference, enabling performance improvement from one trial to the next. The MFG, comprising the visual working memory network and the dorsal attention network (Hammer, Tennekoon, et al., 2015; Gazzaley & Nobre, 2012), might have taken part in circulating task-relevant information, enabling coupling the visual stimuli with the feedback information, which became available only after the stimuli offset.

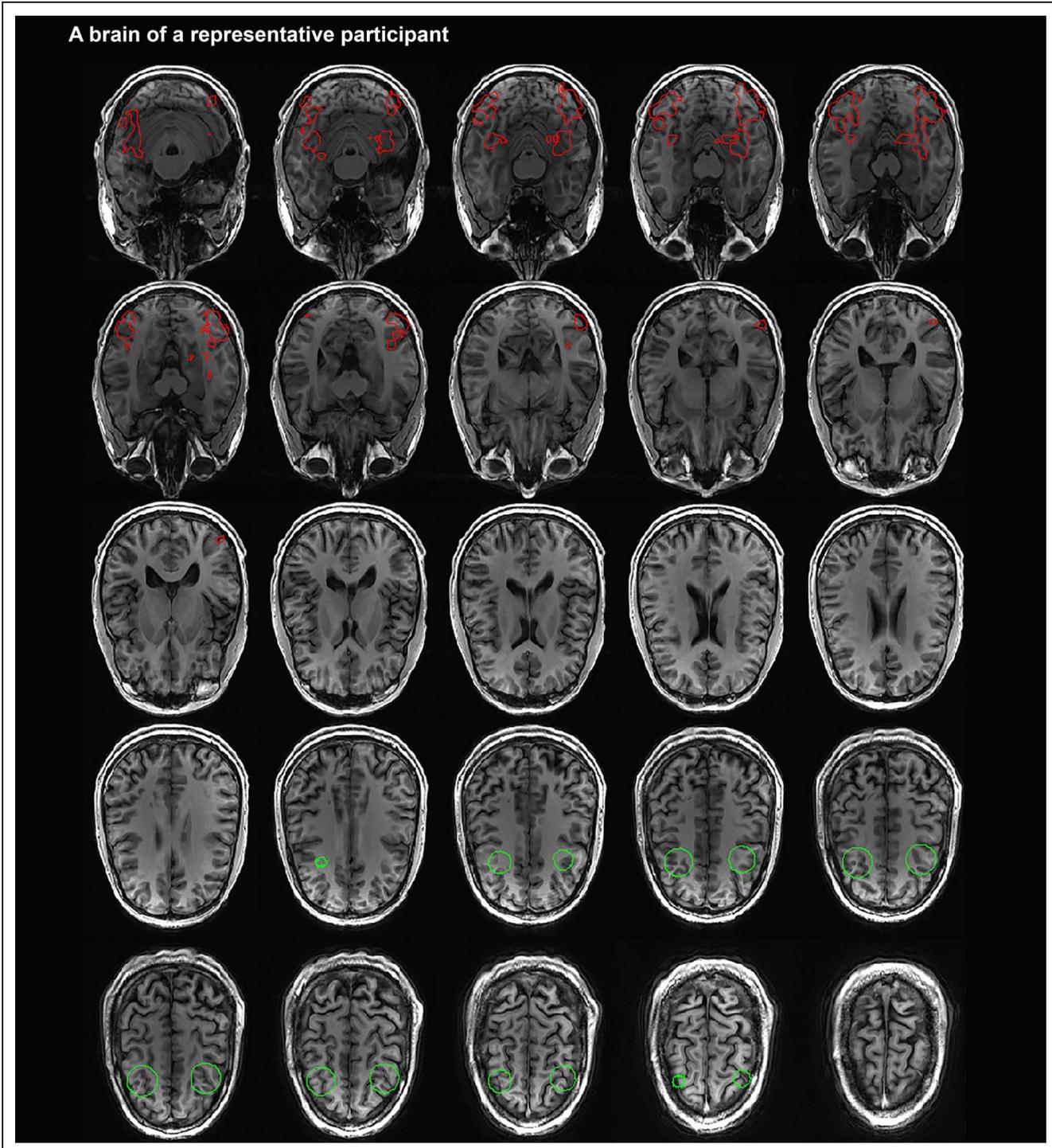
We show that, in VCL tasks with similarly informative and intermixed same-category trials and different-categories trials, distinct trial types are associated with a distinct pattern of brain activation. However, respective roles of same-category comparison and different-categories comparison may differ in scenarios where the primary challenge is learning to distinguish between categories with lower saliency differences. In such VCL tasks, which require perceptual learning (Goldstone, de Leeuw, & Landy, 2015; Hammer, 2015; Watanabe & Sasaki, 2015; Erickson et al., 2005), contrasting objects from different categories would be valuable for highlighting differences between categories (Folstein, Palmeri, & Gauthier, 2014; Folstein et al., 2013; Jiang et al., 2007). That is, lower-saliency VCL tasks may require allocating more cognitive resources when processing perceptually similar stimuli from different categories. This would likely impact activation levels in both executive and early visual cortices, in a way that might be different from what we observed here. Future studies should investigate the prevalence of the current findings in low-saliency VCL scenarios. Furthermore, testing larger number of participants would enable assessing if individual differences in the capacity to allocate more cognitive resources to same-category stimuli in high-saliency VCL tasks, or more resources to different-categories stimuli in low-saliency VCL tasks, account for individual differences in VCL proficiencies and perceptual expertise.

**APPENDIX A: Stimulus Sets Used in the Experiment**



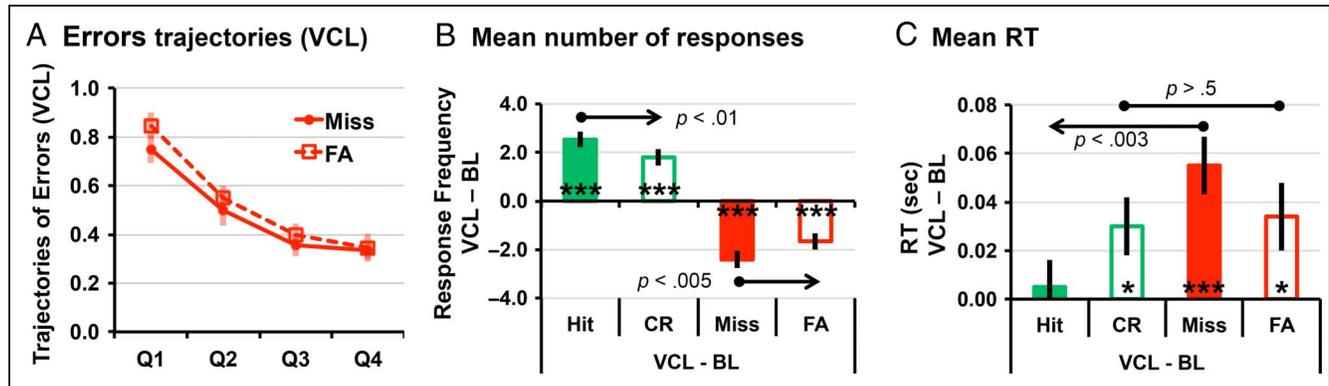
(A) Examples of stimuli used in the experiment. Green = stimuli used in the experimental tasks. Red = stimuli used in the training tasks to familiarize the participants with the experimental procedure. Each stimuli set is represented by two orthogonal stimuli that differ in the three binary feature dimensions. (B) Examples of stimuli used in the functional localizer tasks. On the left column are grayscale versions of stimuli used in the experiment, and on the right column are corresponding phase-scrambled stimuli.

## APPENDIX B: A Representative Participant Brain



LOC (red) ROIs were determined based on a functional localizer, for each participant separately. Talairach coordinates of the MFGs (green), for all participants, were  $[\pm 35, 30, 35]$ .

## APPENDIX C: VCL Performance



(A) Learning trajectories of misses and FAs in the VCL tasks were with a similarly significant monotonic reduction (linear contrast),  $F(1, 13) = 85.39$ ,  $p < .0001$ ,  $\eta_p^2 = 0.87$ , with no significant differences between the two error types,  $F(1, 13) = 0.94$ . (B, C) \* indicating  $<.05$  and \*\*\* indicating  $<.005$  (two-tailed, uncorrected for multiple tests). Although trajectories indicate consistent improvement, categorization errors were evident also in the last quarter of trials, Q4.

	VCL - BL (Response Freq.; B)	VCL - BL (RT; C)
Correctness (error vs. correct)	$F = 43.56$ $p < .0001$	$F = 7.37$ $p < .02$
Category relation (same vs. different)	<i>ns</i>	<i>ns</i>
Correctness by category relation Interaction	$F = 11.32$ $p < .005$	$F = 5.75$ $p < .04$

The Correctness  $\times$  Category relation interaction for categorization accuracy (VCL - BL) was at least partially driven by a response bias in the BL tasks, where participants made more left-key presses (“different categories” decision; CRs and misses) than right-key presses (“same category” decisions). This “different categories” bias was small but statistically significant.

## APPENDIX D: Factorial Analysis for Contrast VCL, Fixation Only

Factorial Analysis for Each ROI in the Stimuli Processing Phase (VCL contrasted with Fixation-Only)

	<i>L-LOC</i>	<i>R-LOC</i>	<i>L-MFG</i>	<i>R-MFG</i>
Correctness (error vs. correct)	$F = 2.00$ $p = .18$	$F = 0.41$ $ns$	$F = 0.71$ $ns$	$F = 0.41$ $ns$
Category relation (same vs. different)	$F = 2.64$ $p = .13$	$F = 5.33$ $p < .04$ $\eta_p^2 = 0.29$	$F = 1.17$ $ns$	$F = 0.29$ $ns$
Correctness $\times$ Category relation Interaction	$F = 0.00$ $ns$	$F = 0.07$ $ns$	$F = 0.08$ $ns$	$F = 0.08$ $ns$

*ns* indicates statistically nonsignificant effects, with  $p \geq .2$ .

Factorial Analysis for Each ROI in the Feedback Processing Phase (VCL contrasted with Fixation-Only)

	<i>L-LOC</i>	<i>R-LOC</i>	<i>L-MFG</i>	<i>R-MFG</i>
Correctness (error vs. correct)	$F = 1.27$ $ns$	$F = 0.17$ $ns$	$F = 26.03$ $p < .001$ $\eta_p^2 = 0.67$	$F = 25.34$ $p < .001$ $\eta_p^2 = 0.66$
Category relation (same vs. different)	$F = 13.15$ $p < .004$ $\eta_p^2 = 0.50$	$F = 9.64$ $p < .01$ $\eta_p^2 = 0.43$	$F = 0.03$ $ns$	$F = 3.36$ $p = .09$ $\eta_p^2 = 0.20$
Correctness $\times$ Category relation Interaction	$F = 3.31$ $p = .09$ $\eta_p^2 = 0.20$	$F = 1.43$ $ns$	$F = 3.59$ $p = .08$ $\eta_p^2 = 0.22$	$F = 0.48$ $ns$

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