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Practiced naming of objects and actions: An fMRI study

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Author contributions: G.M., A.L. and E.D. designed research; E.D. performed research; E.D. analyzed data; A.L. contributed analytic tools; E.D. wrote the first draft of the paper; E.D., A.L. and G.M. edited the paper.

Acknowledgements: Funding for this work was provided by the European Commission within the action 2014—0685/001-001-EMJD, Framework Partnership Agreement 2012-2025 (E.D.), and by the Fondazione CaRiTRo (G.M.). A.L. is supported by a grant from the German Research Foundation (Heisenberg-Professorship, Li 2840/2-1).

Conflict of interest: The authors declare no competing financial interests.

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Abstract

Word retrieval deficits are a common problem in patients with stroke-induced brain damage. While complete recovery of language in chronic aphasia is rare, patients' naming ability can be significantly improved by speech therapy. A growing number of neuroimaging studies have tried to pinpoint the neural changes associated with successful outcome of naming treatment. However, the mechanisms supporting naming practice in the healthy brain have received little attention. Yet, understanding these mechanisms is crucial for teasing them apart from functional reorganization following brain damage. To address this issue, we trained a group of healthy monolingual Italian speakers on naming pictured objects and actions for ten consecutive days and scanned them before and after training. Using a combination of univariate and multivariate analyses, we established that object and action naming evoked different responses in lateral occipitotemporal, posterior parietal and left inferior frontal cortices, largely in line with previous findings. However, training of noun and verb production was associated with similar activation changes, encompassing both anterior and posterior regions of the left hemisphere. We argue that while left anterior activation decreases (posterior inferior frontal gyrus, anterior insula) are likely associated with decreased lexical selection demands, training-related activation changes in left parietal and temporal cortices potentially reflect retrieval of knowledge pertaining to trained items from episodic memory (precuneus, angular gyrus) and facilitated access to phonological word forms (posterior superior temporal sulcus).

Keywords

language training, object naming, action naming, fMRI, MVPA

Significance statement

Folk wisdom says that practice makes perfect. While the truthfulness of this statement might seem trivial, the underlying brain mechanisms are not yet fully understood. Here we investigate the functional plasticity that accompanies practice-related facilitation following training. We measured the fMRI signal during the production of nouns and verbs from pictures before and after two weeks of intensive naming training. Although activity during object vs. action naming dissociated in a number of regions, training effects for the two word classes were similar and encompassed activation decreases in classical language regions of the left prefrontal cortex. Additionally, MVPA revealed training-related activation changes in posterior areas of the left hemisphere implicated in phonological word storage and episodic memory.

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Introduction

Attempted naming can improve performance in aphasic individuals even in the absence of feedback or corrections (Howard, 2000; Nickels, 2002). Although the neural mechanisms underlying this improvement are not clear, it has been recently suggested that they may at least partially overlap with those that support naming facilitation in healthy controls (Heath et al., 2015; Kurland et al., 2018). Thus, identifying the neural changes induced by training in healthy participants is necessary to establish a "baseline", against which the results of anomic patients could be compared.

Studies of incidental naming practice show that even a single instance of naming in the context of a picture naming task can facilitate subsequent processing of a stimulus for days and even weeks (van Turennout et al., 2000, 2003; Meister et al., 2005). While behaviorally this effect, known as repetition priming, manifests itself as shorter naming latencies, at the neural level it is reflected by decreased activity (or "repetition suppression") in bilateral occipitotemporal and left prefrontal cortices, associated with facilitated perceptual/conceptual and linguistic processing of the stimulus respectively.

The effects of explicit naming practice were addressed by Basso et al. (2013), who used an intensive training paradigm, more closely resembling speech therapy in patients. Explicit training of object naming (ten repetitions per day over ten consecutive days) was associated with a decreased BOLD response in the left inferior frontal cortex and the fusiform gyrus, in line with studies on repetition suppression, and with increased response in the precuneus and the posterior cingulate cortex. Increased activation of the medial parietal areas, which are not involved in the classic language network, was attributed to retrieval of memories related to practiced items from long-term memory. Similar findings were reported by MacDonald et al. (2015) in healthy older adults, who showed increased activity in the precuneus and decreased activity in the inferior frontal and inferior temporal cortices bilaterally following two object naming sessions (three repetitions/session).

Practice-related activation changes could be modulated by a number of factors (intensity of practice, interval between stimulus repetitions, etc.). Yet, one critical factor, namely, the content of training, has received little attention. Most studies have focused on practiced naming of objects, that are referred to by nouns. Neuropsychological findings (for reviews, see Cappa and Perani, 2003; Mätzig et al., 2009), as well as recent neuroimaging studies with healthy individuals (for reviews, see Crepaldi et al., 2011; Vigliocco et al., 2011) suggest that words belonging to different grammatical classes, such as nouns and verbs, may have at least partially dissociable neural correlates. Thus, it seems reasonable to expect them to be differently affected by practice. A recent study by Kurland et al. (2018) attempted to address this question by including both nouns and verbs in their training protocol, but failed to find a significant interaction between training and word class. It is possible, however, that these null results were due to low intensity of practice (five repetitions a few days prior to the fMRI session, plus five repetitions immediately before the scanning).

In the present fMRI study we investigated differences in the magnitude and localization of training effects for nouns and verbs. Healthy speakers of Italian practiced naming of objects and actions for ten consecutive days and were tested twice, on the days preceding and following the training (see Figure 1). The two experimental sessions were identical and included trained items, as well as an

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equal number of untrained items that served to control for task habituation and priming effects. The use of this paradigm allowed us to (1) scrutinize the putative distinctions in the neural representations of objects (nouns) and actions (verbs), (2) investigate the effects of training and their potential interaction with word class, and (3) evaluate the reliability of long-term priming effects reported in previous studies (Meister et al., 2005; Meltzer et al., 2009) and set them apart from the effects of explicit training.

Materials and Methods

Participants

A total of 35 native Italian speakers took part in this project — 12 subjects (3 male, mean age: 23.3 ± 2.5 years, age range: 19-28 years) participated in the behavioral study, and 23 (9 male, mean age: 23.7 ± 3.3 years, age range: 19-32 years) in the fMRI study. Three subjects of the fMRI study were subsequently excluded from data analyses — two because of excessive head motion during scanning (more than 3 mm in one of the directions) and one due to non-compliance with the training protocol. All participants but one were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971); the remaining subject was a self-reported right-hander, but scored as ambidextrous on the Inventory. All participants had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disease.

The study was conducted in compliance with the Declaration of Helsinki and was approved by the Human Research Ethics Committee of the University of Trento. All participants signed informed consent forms.

Stimuli

Preliminary naming task. All participants of the behavioral (N = 12) and the fMRI (N = 23) study were required to undergo the preliminary naming task prior to entering the two-session training study, in order to assure that they recognized objects and actions that would be presented in the two experimental sessions and retrieved their corresponding names. Stimuli consisted of line drawings of 80 objects and 80 actions that were presented at a comfortable pace using PowerPoint. Subjects were instructed to produce names of objects using an Italian noun in a singular form (without an article) and to produce names of actions using a verb in the infinitive form. Part of the stimuli were specifically drawn for the present study, while others were selected from various sources, including the Verb and Action Test (VAT; Bastiaanse et al., 2016), the Battery for the Analysis of Aphasic Deficits (BADA; Miceli et al., 2001), as well as the public domain (see examples of drawings in Figure 1).

Experimental naming task. Of the 160 drawings presented in the preliminary task, 40 object and 40 action pictures were used in two identical experimental naming sessions. Half of the items in each set were included in the training protocol, while the other half were not explicitly trained and served as controls for potential stimulus priming/task habituation effects. The four resulting 20-item subsets

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— untrained nouns (NU), trained nouns (NT), untrained verbs (VU) and trained verbs (VT) — were matched for variables that reportedly affect word retrieval. Words in the four subsets were balanced for phonemic ($H(3) = .43$, $p = .934$) and syllabic ($H(3) = .804$, $p = .848$) length, as well as for relative lemma frequency ($H(3) = .006$, $p = .996$), based on a lexical database of written Italian (Corpus e Lessico di Frequenza dell'Italiano Scritto, CoLFIS; http://linguistica.sns.it/CoLFIS/Home.htm). Online questionnaires, created on the website SurveyMonkey.com, were delivered to separate groups of Italian native speakers in order to balance target words for familiarity (60 participants; $H(3) = 2.629$, $p = .452$), imageability (38 participants; $H(3) = 6.549$, $p = .088$) and subjective age of acquisition (55 participants; $H(3) = 3.473$, $p = .324$). Another questionnaire was used to balance naming agreement of pictorial stimuli (48 participants; $H(3) = 2.158$, $p = .54$). Additionally, pictures were matched for objective visual complexity ($H(3) = .245$, $p = .97$) using the GIF lossless compression method (Forsythe et al., 2008). Nouns were selected from a broad range of semantic categories, including animals, professions, clothing, furniture, buildings, vehicles, fruit and vegetables. Verbs were roughly matched for transitivity (VT: 11 transitive, 9 intransitive; VU: 11 transitive, 9 intransitive) and instrumentality (VT: 10 instrumental, 10 non-instrumental; VU: 9 instrumental, 11 non-instrumental). Pictures were normalized with an average brightness of 128 cd/m^2. Fourier-transformed phase-scrambled images were additionally introduced into the experimental set as low-level controls. In the second experimental session all images were flipped horizontally in order to reduce potential effects of priming in early visual areas.

Training materials. Subjects were asked to practice overt naming of 20 objects in the NT subset and 20 actions in the VT subset, using ten booklets with color photographs (one for each day of training). Photos were taken from the public domain and represented various depictions of to-be-trained objects and actions (see Figure 1 for examples). Each booklet contained a different exemplar of the same concept, in order to tap into abstract structural representations rather than low-level perceptual features. A booklet was divided into two sections — "Objects" and "Actions". Items within each section were presented in random order.

Procedure

The experimental paradigm is schematically depicted in Figure 1. Subjects underwent intensive naming training for ten consecutive days (excluding weekends). The training material consisted of 20 objects (NT subset) and 20 actions (VT subset). Training was carried out at home, at a time comfortable for a subject. To make sure that participants complied with the training protocol, they were asked to record their responses with the help of a digital recorder. A daily training session consisted of naming all objects and actions in a given booklet for ten times.

All subjects completed two identical experimental sessions — one before and one after the training. Since participants of the fMRI study were instructed to remain silent inside the scanner during picture presentation (in order to avoid jaw movement artifacts) and to overtly respond when they saw the next slide, we gathered reaction time (RT) data from a separate group of N = 12 volunteers who participated in an analogous experiment in which they were asked to produce a word as soon as

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they saw a picture. In addition to the 40 trained objects and actions (NT and VT subsets), participants were presented with an equal number of untrained items (NU and VU subsets). Their task was to name the depicted object or action aloud, using a single Italian word (a noun without an article, a verb in the infinitive form). Whenever a scrambled image appeared, subjects were instructed to produce a pseudoword — */ber.'to:va/* (in session 1) or */sin.'to:ti/* (in session 2).

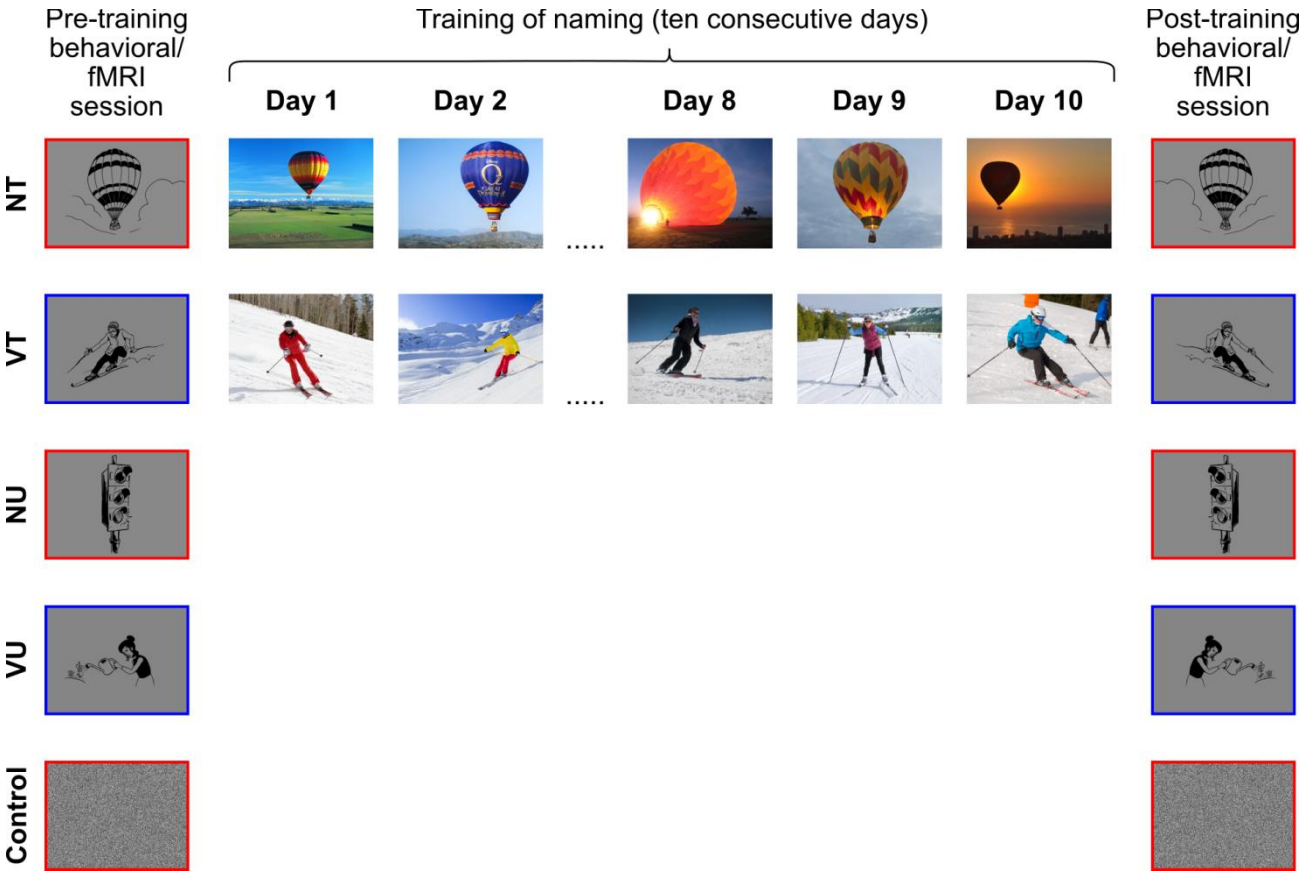

Figure 1. The experimental paradigm. Participants of the behavioral and the fMRI studies named color photographs of 20 objects (NT) and 20 actions (VT) for ten consecutive days. Before and after the training program, they underwent two identical experimental naming sessions that included trained items (NT and VT), as well as an equal number of untrained nouns (NU) and untrained verbs (VU), used as controls for potential stimulus/task habituation effects. Fourier-transformed phase-scrambled images (Control), in response to which subjects were instructed to produce a pseudoword, were also presented in both studies.

Stimuli were presented in a blocked design. A run consisted of four blocks — NU, NT, VU and VT — presented in random order. Each block included five items belonging to one of the four experimental conditions, as well as two randomly interspersed scrambled images. Word class was cued by a colored frame around an image: a red frame for nouns (NU and NT blocks), a blue frame for verbs (VU and VT blocks). A frame was also placed around scrambled images that appeared within a noun or a verb block. Subjects were instructed to produce the same pseudoword irrespective of frame color. All stimuli (n = 80) were presented within four experimental runs, and

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subsequently repeated within four additional runs in a different order. Due to technical reasons, for one of the participants of the fMRI study only four out of eight runs were acquired in the first experimental session.

Prior to each experimental session, participants received written instructions and underwent short practice. Stimulus presentation and response collection were controlled with ASF (Schwarzbach, 2011), a toolbox based on Psychtoolbox-3 (Brainard, 1997; RRID: SCR_002881) for MATLAB (MathWorks; RRID: SCR_001622).

Experimental design

Behavioral naming study (N = 12 participants). The first experimental session took place on the day after the preliminary naming task. Training started 1 to 3 days after the first experimental session (mean: 1.9 days) and finished on the day preceding the second experimental session. Subjects were allowed to refrain from training during weekends (mean: 2 days). Each trial started with a 2 s black fixation cross followed by a 3 s picture presentation. The inter-trial interval (ITI) was set to 1 s. Blanks of 5 s were introduced between blocks, and at the beginning and the end of each run. Subjects were asked to reply as soon as they saw a picture. Stimuli were presented on an LCD screen with the resolution of 1920 × 1080 pixels and the frame rate of 60 Hz.

fMRI naming study (N = 23 participants). The preliminary naming task was administered 1 to 4 days prior to the first fMRI session (mean interval: 1.5 days). The training procedure started 1 to 4 days after the first fMRI session (mean: 1.9 days) and finished on the day preceding the second fMRI session. Subjects were allowed to take 1-4 days of rest from training (mean: 2.2 days). Each trial started with a black fixation cross whose presentation lasted between 2 and 5 s. The duration of the initial fixation was chosen from a geometric distribution (p = .4; in steps of 1 s). The fixation cross was followed by a picture, presented for 2 s. Subjects were instructed to withhold overt responses while viewing the picture and to respond when a green fixation cross following the picture appeared (3.5 s). The ITI was jittered between 0.5 and 1 s (in steps of 0.25 s). Blanks with a duration of 6 s were introduced between blocks. Each run started and ended with a 12 s blank. In the scanner, stimuli were back-projected onto a screen (frame rate: 60 Hz, screen resolution: 1024 × 768 pixels) via a liquid crystal projector (OC EMP 7900, Epson, Japan). Participants viewed the screen binocularly through a mirror mounted on the head coil.

Data acquisition

Behavioral data acquisition. Vocal responses of the participants of the behavioral study were collected using the Samson Q4 microphone with a low-noise microphone cable (Thomann, UK). RTs were measured automatically using the voice key function supplied with ASF. Recordings were digitized at a sampling rate of 44.1 kHz.

MR data acquisition. Neuroimaging data were collected at the Functional Neuroimaging Laboratories (LNiF) of the Center for Mind/Brain Sciences (CIMeC) at the University of Trento,

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Italy, using a 4T Bruker MedSpec MR scanner with an 8-channel birdcage head coil. Functional images were acquired using a T2*-weighted gradient echo-planar imaging (EPI) sequence with fat suppression. Scanning was performed continuously during a functional run with the following parameters: repetition time (TR) = 2.2 s, echo time (TE) = 33 ms, flip angle (FA) = 75˚, field of view (FOV) = 192 × 192 mm, matrix size = 64 × 64, voxel resolution = 3 × 3 × 3 mm. We acquired 31 slices in ascending-interleaved odd-even order, with a thickness of 3 mm and a 15% gap (0.45 mm). Slices were aligned to the AC-PC plane. An imaging volume was positioned to cover the entire temporal lobe; as a result, a small portion of the superior parietal cortex was not captured in most subjects. The number of volumes in a functional run varied (range: 130-142) as a result of temporal jittering introduced into trials. Before each run we performed an additional scan measuring the point-spread function (PSF) of the acquired sequence, in order to correct the distortion in geometry and intensity expected with high-field imaging (Zeng and Constable, 2002; Zaitsev et al., 2004). A T1-weighted structural scan at the beginning of each scanning session served as reference for coregistration of functional data. Structural images were acquired using a magnetization-prepared rapid-acquisition gradient echo (MPRAGE) sequence (TR = 2.7 s, TE = 4.18 ms, FA = 7˚, FOV = 256 × 224 mm, 176 slices, inversion time (TI) = 1020 ms), with generalized autocalibrating partially parallel acquisition (GRAPPA) with an acceleration factor of 2.

Data analysis

Behavioral data analysis. Voice onset intensity threshold was calibrated for each subject based on the visual inspection of the wave plots of vocal responses with displayed RTs at a given threshold produced by the ASF software for each trial. RTs deviating from a subject's mean by more than two standard deviations were considered outliers and removed from analysis (5.2% of the data removed, including 3.4% of object trials, 9.9% of action trials and 1.4% of control trials). After calculating individual descriptive statistics in MATLAB R2015b, data were submitted to inferential analysis with repeated-measures ANOVAs and paired-samples *t*-tests in SPSS 24 (RRID: SCR_002865).

Preprocessing of MR data. Neuroimaging data were preprocessed and analyzed using BrainVoyager QX 2.8.4 (Brain Innovation; RRID: SCR_013057) in combination with the NeuroElf toolbox (v. 1.1; RRID: SCR_014147) and in-house software written in MATLAB. The first three volumes of a functional run were discarded to avoid T1 saturation. For each run, we performed slice timing correction (cubic spline interpolation), followed by 3D motion correction (trilinear interpolation for estimation and sinc interpolation for resampling, all functional volumes acquired in a session realigned to the first volume of the first run) and temporal high-pass filtering with linear trend removal (cut-off frequency of 3 cycles per run). For univariate analyses, functional data were spatially smoothed with a Gaussian filter of 6 mm full width at half maximum (FWHM), in order to reduce noise and minimize intersubject anatomical differences. Functional and structural data were aligned in several steps, using the rigid-body transformation with 6 parameters (3 translations, 3 rotations): the first volume of the first functional run in a session was coregistered to an anatomical image for the corresponding session; then, anatomical scans obtained in the two sessions with a participant were aligned to each other; finally, functional data from both sessions were coregistered

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to one of the anatomical images using the transformation parameters obtained during the intersession anatomical alignment. For group analysis, structural and functional data were standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988), using sinc interpolation.

GLM. Statistical analyses were performed with a general linear model (GLM), as implemented in BrainVoyager. A trial was modeled as an epoch lasting from the onset to the offset of a picture (2 s). Regressors included predictors of the 10 experimental conditions (2 sessions × 5 conditions: S1_NU, S1_NT, S1_VU, S1_VT, S1_Control, S2_NU, S2_NT, S2_VU, S2_VT, S2_Control). Additionally, 6 parameters resulting from head motion correction were included in the model as regressors of no-interest. Each predictor was convolved with a dual-gamma hemodynamic response function (HRF; Friston et al., 1998). The resulting reference time courses were used to fit the signal time courses in each voxel.

Cortex-based alignment. Analyses were performed on the cortical surface, with the help of cortex-based alignment (CBA) as implemented in BrainVoyager. This procedure enables better alignment of structural and functional data across subjects by taking into account individual variability in gyral and sulcal folding patterns. To this end, we segmented the white/gray matter boundary on individual Talairach-transformed T1-weighted anatomical scans and reconstructed 3D hemispheric meshes for each participant. Then we inflated each mesh to a sphere with cortical curvature maps projected onto it (with four coarse-to-fine levels of smoothing) and aligned it to a standard spherical surface using a coarse-to-fine moving target approach (Fischl et al., 1999; Goebel et al., 2006). The resulting transformation matrices were used to create group-averaged surface meshes for the left and the right hemisphere. Statistical analyses were performed separately for each hemisphere. Thresholded statistical maps obtained for a group were projected onto the group-averaged hemispheric meshes for visualization and described using the CBA-transformed macroanatomical surface atlases supplied with BrainVoyager.

Univariate analysis. For the univariate analysis, we created mesh time courses for each run by sampling the spatially smoothed functional data from -1 to 2 mm from the reconstructed white/gray matter boundary. For the first level analysis (prior to CBA), we ran individual fixed-effects (FFX) GLMs on the subject data collapsed across runs and obtained *t*-statistics for main effects of the experimental conditions. These *t*-maps were subsequently aligned to group-averaged meshes using the aforementioned transformation matrices. At the group level, individual CBA-transformed *t*-maps were submitted to nonparametric permutation testing (Nichols and Holmes, 2002), in combination with Threshold-Free Cluster Enhancement (TFCE; Smith and Nichols, 2009) as implemented in the CoSMoMVPA toolbox (Oosterhof et al., 2016; RRID: SCR_014519). A total of 1000 Monte Carlo simulations and a corrected cluster threshold $\alpha = .05$ (two-tailed; $z > 1.96$) were used.

MVPA. In addition to the standard whole-brain GLM, we carried out multivariate pattern analysis (MVPA; Haxby et al., 2001). Rather than contrasting the amplitude of the BOLD response in individual voxels/surface vertices, MVPA is based on comparing spatial patterns of activation in response to different experimental conditions (for review, see Haxby, 2012). Specifically, we employed a whole-brain searchlight analysis, a recently developed MVPA technique for identifying

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locally informative areas of the brain (Kriegeskorte et al., 2006; Etzel et al., 2013), which may outperform mass-univariate analyses due to its greater sensitivity to distributed coding of information (Jimura and Poldrack, 2012; Davis et al., 2014). We performed a searchlight analysis on the brain surface (Oosterhof et al., 2011), using a linear discriminant analysis (LDA) classifier, as implemented in CoSMoMVPA. We aimed to examine in which areas the classifier could reliably (i.e., significantly above chance) distinguish: (1) nouns vs. verbs (using data from the pre-training fMRI session), and (2) trained vs. untrained items (based on data from the post-training fMRI session). To this end, we ran single-study GLMs separately for each run of each subject, using unsmoothed mesh time courses. At the single-subject level (prior to CBA), maps containing *t*-statistics for the main effects of experimental conditions for each run in a session were stacked together and submitted to the searchlight analysis across the entire cortex using spheres with an 8-mm radius. Classification accuracies were obtained using a leave-one-out cross-validation method with an 8-fold partitioning scheme. The dataset was split into 8 chunks (each corresponding to one experimental run), and the classifier was trained on the data from 7 chunks and tested on the remaining one. The procedure was repeated for 8 iterations, using all possible train/test partitions, and the average decoding accuracies across these iterations were calculated. Decoding accuracies obtained for a given searchlight were assigned to its central vertex. Individual surface maps containing average decoding accuracies were aligned to the group-averaged mesh using the transformation matrices obtained during CBA. At the group level, a two-tailed one-sample *t*-test across individual maps identified vertices where classification was significantly above chance (50%, since our classifiers were binary). The resulting maps were corrected using TFCE with 1000 Monte Carlo simulations (corrected cluster threshold $\alpha = .05$, two-tailed; $z > 1.96$).

Results

Behavioral results

Average response latencies of the 12 participants in the behavioral experiment are presented in Figure 2. A three-way repeated-measures ANOVA with session (first, second), word class (noun, verb) and training (trained, untrained) as within-subject factors was carried out. Significant main effects of word class (faster RTs to nouns than verbs; $F(1, 11) = 68.89$, $p < .001$), training (faster RTs to trained than untrained items; $F(1, 11) = 41.22$, $p < .001$) and session (faster RTs in session 2 than in session 1; $F(1, 11) = 6.32$, $p = .029$) were found. The session-by-training interaction was also significant ($F(1, 11) = 10.57$, $p = .008$) — an expected outcome, considering that prior to training untrained and to-be-trained items were indistinguishable. The lack of significant training-by-word-class ($p = .199$, ns) and session-by-word-class ($p = .285$, ns) interactions suggests the magnitude of training and session effects was similar for words belonging to both classes.

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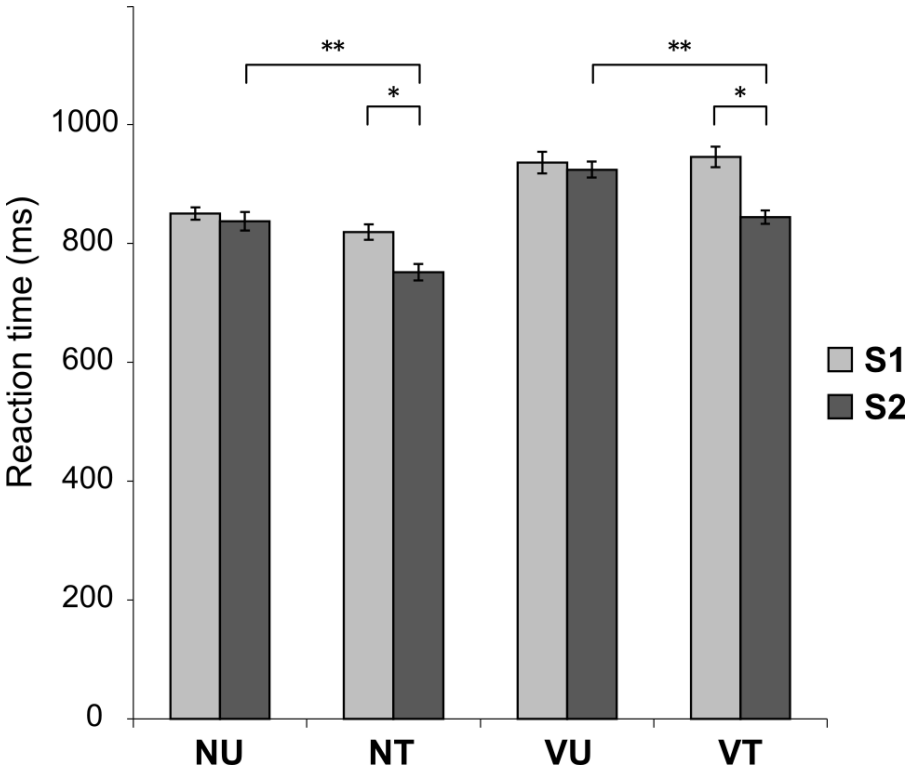

Figure 2. Behavioral results. Average reaction times for each stimulus category in session 1 (S1; light gray bars) and session 2 (S2; dark gray bars). NU = untrained nouns, NT = trained nouns, VU = untrained verbs, VT = trained verbs. Error bars reflect standard errors of the mean after removing between-subject variability (Cousineau, 2005); * denotes significant effects at $p_{FDR} < .05$; ** denotes significant effects at $p_{FDR} < .005$.

To examine whether shorter RTs in the second session were driven mainly by session or by training effects, we conducted six paired-samples *t*-tests comparing trained and untrained items belonging to the same word class within and across sessions. In addition, to rule out significant differences between subsets prior to training, we carried out a *t*-test comparing items from the trained and the untrained subset in session 1 for each word class. The resulting *p*-values were corrected using the false discovery rate (FDR) method for the overall number of comparisons (n = 8; Benjamini and Yekutieli, 2001). The *t*-tests designed to compare the two subsets of nouns and verbs prior to training failed to distinguish RTs to to-be-trained and not-to-be-trained items (nouns: S1_NT vs. S1_NU: $p = .154$, ns; verbs: S1_VT vs. S1_VU: $p = .611$, ns). Significant effects of training, for both nouns and verbs, were observed when comparing responses to trained items before and after training (S2_NT vs. S1_NT: $p_{FDR} = .026$; S2_VT vs. S1_VT: $p_{FDR} = .01$), and responses to trained and untrained items after training (S2_NT vs. S2_NU: $p_{FDR} = .003$, S2_VT vs. S2_VU: $p_{FDR} = .004$). However, no significant session effects were found for untrained nouns (S2_NU vs. S1_NU: $p_{FDR} = .694$, ns) and verbs (S2_VU vs. S1_VU: $p_{FDR} = .645$, ns), suggesting that the significant main effect of session had been actually driven by the training effect.

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fMRI results: word class effects

Univariate results

Naming of pictured objects and actions activated similar brain networks (Figure 3*A*; Supplementary Table 1), as shown by contrasting nouns/verbs with phase-scrambled controls in the first fMRI session (S1_NU + S1_NT > S1_Control; S1_VU + S1_VT > S1_Control). Activations were observed bilaterally in ventral and lateral occipitotemporal areas, including inferior and middle occipital gyri, fusiform and parahippocampal gyri, i.e., in the ventral visual processing stream involved in object and shape recognition (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992, 2018). They extended bilaterally into the posterior portion of the superior parietal lobule (SPL) and anterior insular cortices. Additionally, picture naming recruited most of the left inferior frontal gyrus (IFG), as well as the ventral precuneus and pre-supplementary motor area (pre-SMA). Inspection of Figure 3*A* suggests that bilateral activations associated with verb production were more extensive than those associated with noun production in posterior middle temporal gyri (pMTG) and SPL. The direct contrast of responses to nouns and verbs in session 1 (S1_VU + S1_VT > S1_NU + S1_NT; Figure 3*B*; Supplementary Table 2) revealed that verb naming engaged to a significantly greater extent the lateral occipitotemporal cortices (LOTC), as well as regions in the left SPL and intraparietal sulcus. The opposite contrast (S1_NU + S1_NT > S1_VU + S1_VT) detected a stronger BOLD response for nouns than verbs only in a small cluster in the posterior portion of the medial fusiform/extrastriate cortex.

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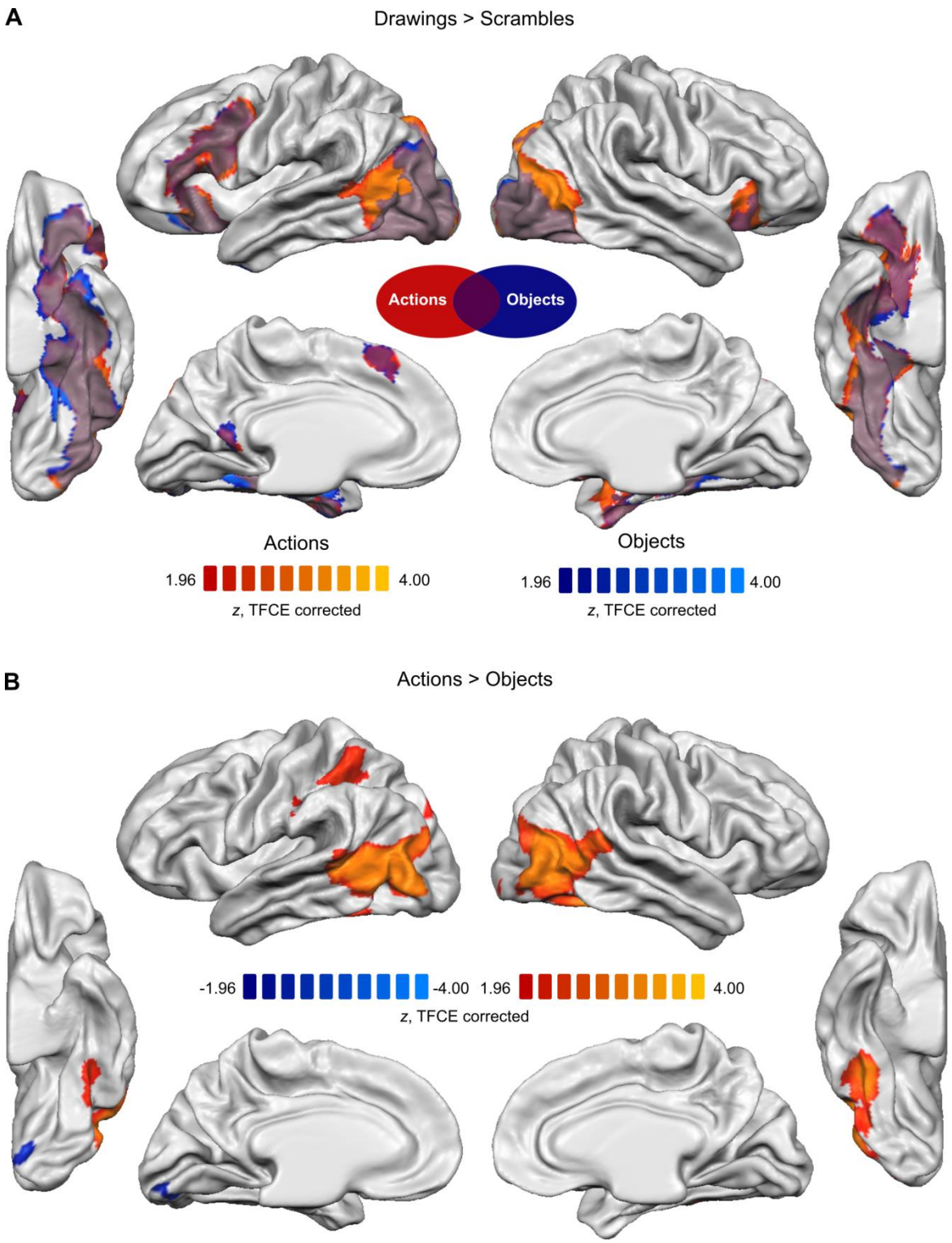

Figure 3. Word class effects, revealed by the univariate RFX GLM contrasts of stimuli presented in the pre-training fMRI session. *A,* Object (blue) and action (red/orange) naming networks, identified by contrasting all nouns/verbs with meaningless scrambled images (negative tail not shown). The logical conjunction of the two maps (i.e., areas recruited both during object and action naming) is indicated in purple. *B,* Areas showing increased BOLD response to verbs as compared to nouns (red/orange) and to nouns as compared to verbs (blue). The statistical group maps (N = 20) for each hemisphere were corrected for multiple comparisons using TFCE (α = .05, two-tailed) and projected onto the group-averaged surface meshes for visualization.

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MVPA results

We trained the classifier on data from the pre-training fMRI session to identify areas in which it would reliably distinguish nouns and verbs. The whole-brain searchlight analysis (Figure 4; Supplementary Table 3) showed that patterns of *t*-scores for nouns and verbs were decoded in a number of bilateral areas, including LOTC and SPL, confirming findings of the univariate analysis. Nouns and verbs were also distinguishable on the basis of their patterns of activation in ventral occipitotemporal cortices, early visual areas and precuneus. Finally, we were able to decode nouns and verbs in the left IFG, extending dorsally into the middle frontal gyrus and caudally into the premotor cortex.

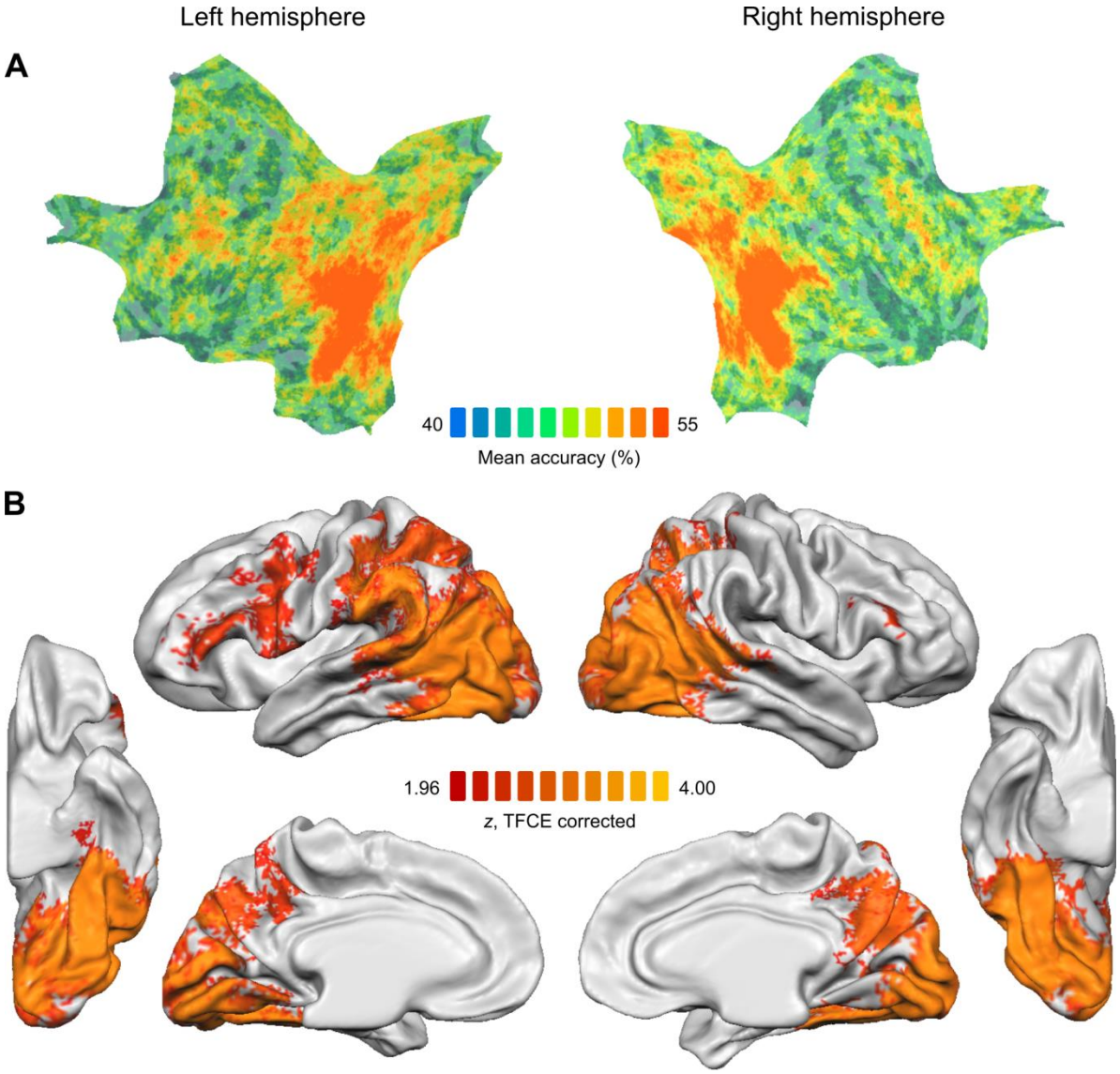

Figure 4. Decoding of word classes (nouns vs. verbs), based on the pre-training fMRI session. ***A,*** Mean accuracy maps of the searchlight MVPA. Individual accuracy maps (N = 20) were averaged and projected onto a flattened group-averaged hemispheric surfaces. Chance accuracy is 50%. ***B,*** Statistical group maps, corrected using TFCE at α = .05 (two-tailed).

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fMRI results: training effects

Univariate results

To identify the neural correlates of intensive naming practice, we compared responses to trained and untrained items. No significant differences were found when contrasting these items in the first, pre-training fMRI session (S1_NT > S1_NU; S1_VT > S1_VU), attesting to the fact that the two subsets of nouns and the two subsets of verbs had been matched for the relevant variables. In the second, post-training fMRI session, contrasting the same items (S2_NT > S2_NU; S2_VT > S2_VU) revealed significant BOLD amplitude changes in several brain regions (Figure 5*A*; Supplementary Table 4). When compared to untrained items in the same post-training session, both trained nouns (Figure 5*A*, left panel) and trained verbs (Figure 5*A*, right panel) yielded a significantly reduced BOLD response in anterior regions of the left hemisphere, including the posterior IFG (pars opercularis and pars triangularis) and the adjacent frontal operculum/anterior insula. Even though deactivations seemed more extensive for verbs than for nouns, the compound contrast (S2_VT > S2_VU) > (S2_NT > S2_NU) failed to reach significance.

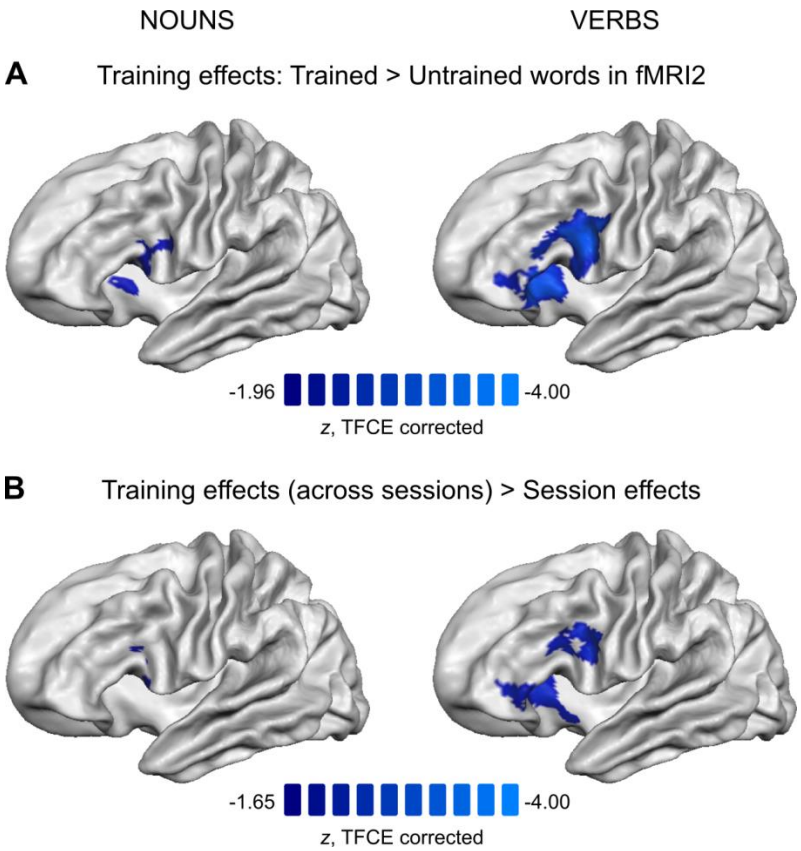

Figure 5. Training effects, revealed by the univariate RFX GLM analysis (N = 20), projected onto the group-averaged mesh of the left hemisphere. ***A,*** Areas showing significant deactivation following training of nouns (left panel) and verbs (right panel), as evidenced by contrasting words from trained and untrained subsets in the post-training fMRI session (corrected using TFCE at α = .05, two-tailed). ***B,*** Comparison of training and session effects across the two fMRI sessions (corrected using TFCE at α = .05, one-tailed), separately for nouns (left panel) and for verbs (right panel).

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Additionally, we examined the effects of incidental word repetition (i.e., session effects), in order to subsequently compare them with the effects of explicit naming practice (i.e., training effects). By contrasting untrained items in the post- and pre-training sessions (Supplementary Figure 1; Supplementary Table 5), we found that the mere exposure to the same stimuli and the same task (in the same scanner environment) twice over the course of two weeks yielded significant repetition suppression in early visual areas and the fusiform, both for nouns (S2_NU > S1_NU; Supplementary Figure 1*A*) and for verbs (S2_VU > S1_VU; Supplementary Figure 1*B*), in line with reports on priming of low-level features and amodal structural representations respectively (for reviews, see Schacter and Buckner, 1998; Henson, 2003). Decreased activity in the SPL (bilateral for nouns, right-lateralized for verbs) was not expected, but could be explained by facilitated visuospatial processing of familiar stimuli (Nobre et al., 1997; Corbetta and Shulman, 1998; Beauchamp et al., 2001). Additionally, a significantly reduced BOLD response for nouns was observed in the left posterior superior frontal gyrus (on the lateral surface, adjacent to the precentral gyrus). The compound contrast (S2_VU > S1_VU) > (S2_NU > S1_NU) failed to reveal significantly different session effects for the two word classes.

Finally, we directly compared the across-session training and session effects (Figure 5*B*; Supplementary Table 6). Since we hypothesized that the BOLD amplitude would decrease more for trained items in the areas associated with explicit practice, we used a one-tailed *t*-test ($z < -1.65$). Indeed, verb training was associated with significantly stronger decrease of the BOLD signal in the left posterior IFG, including a cluster encompassing most of the pars opercularis and a portion of the pars triangularis, as well as clusters in the pars orbitalis and the anterior insula ((S2_VT > S1_VT) > (S2_VU > S1_VU); Figure 5*B*, right panel). An analogous contrast for nouns ((S2_NT > S1_NT) > (S2_NU > S1_NU); Figure 5*B*, left panel) revealed greater training-related reductions of the BOLD response in the left pars triangularis and the adjacent frontal operculum.

MVPA results

To further localize areas sensitive to training, we performed searchlight pattern classification analysis on data from the post-training fMRI session. As a first step, the two classifiers learned to distinguish between trained and untrained items, separately for nouns and verbs. Average decoding accuracies did not go beyond chance in any brain region, possibly due to insufficient statistical power. In order to increase the power, data were collapsed across word classes and a binary classifier was trained to distinguish between trained and untrained items, irrespective of word class. Results (Figure 6; Supplementary Table 7) show that several areas in the left hemisphere (posterior superior temporal sulcus, angular gyrus, precuneus) were sensitive to training. Decoding was also significantly above chance in the left anterior insula (replicating the univariate results) and in two small clusters close to the right calcarine sulcus.

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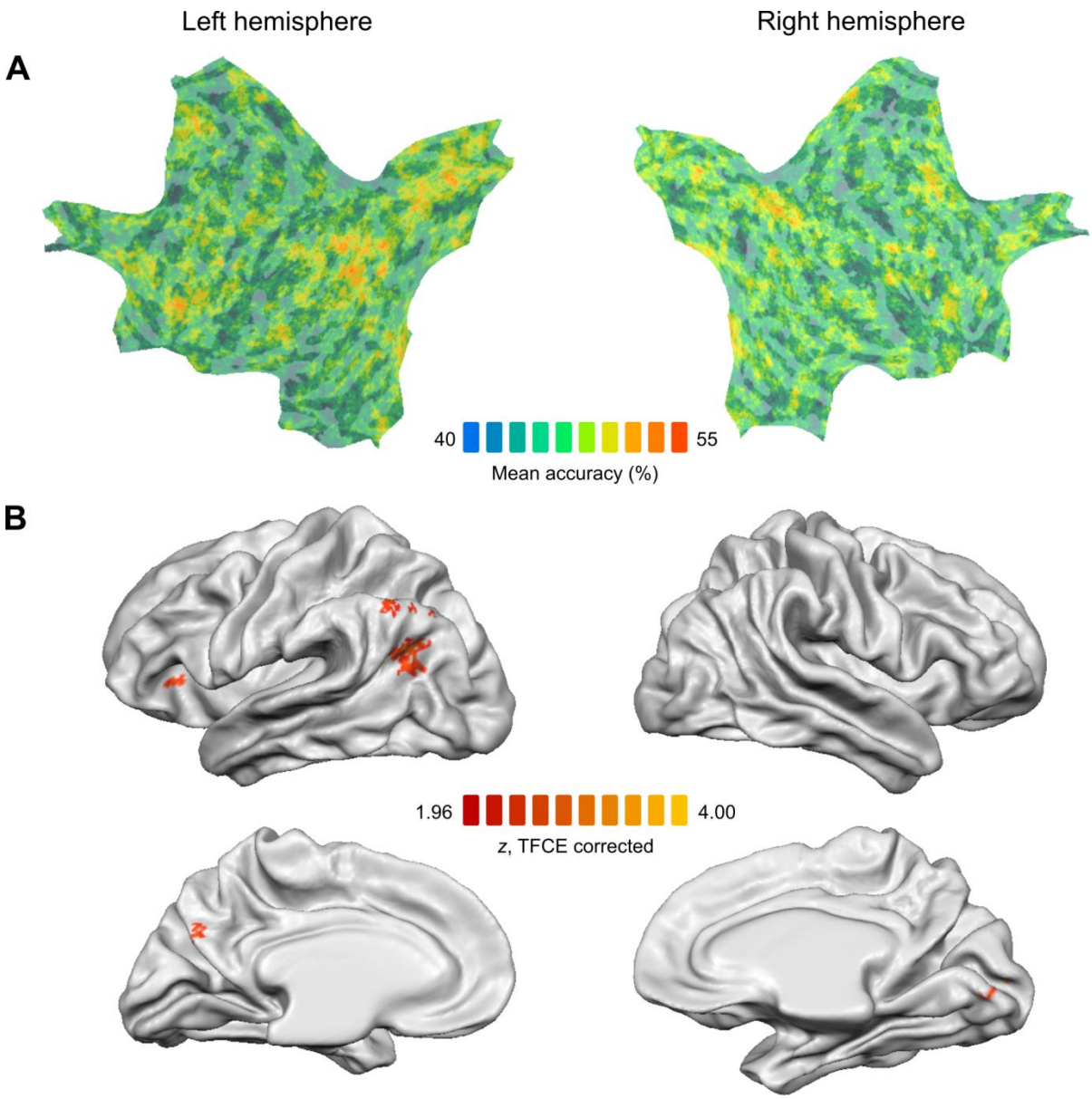

Figure 6. Decoding of trained vs. untrained items, based on data from the post-training fMRI session. ***A,*** Mean accuracy maps of the searchlight MVPA. Individual accuracy maps (N = 20) were averaged and projected onto a flattened group-averaged surface. Decoding accuracy at chance is 50%. ***B,*** Statistical group maps, corrected using TFCE at α = .05 (two-tailed).

Discussion

We examined the mechanisms underlying naming practice of pictures of objects and actions in healthy participants. Nouns and verbs that were trained for ten days were named significantly faster in the post-training session, attesting to the efficiency of training. Naming of objects and actions was associated with significantly different behavioral and neural responses. Collapsing across word classes, training involved both anterior and posterior regions of the left hemisphere. Below we will discuss these observations in more detail.

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Word class effects

Verbs were produced significantly slower than nouns, in line with previous reports (Vigliocco et al., 2004; Kurland et al., 2018). Converging evidence from univariate and multivariate fMRI analyses points to the bilateral LOTC and predominantly left parietal regions as the potential neural loci of word class effects. Increased recruitment of the LOTC by verbs compared to nouns agrees with the role attributed to this area in storing representations of action concepts (for review, see Lingnau and Downing, 2015). Notably, verb-preferring LOTC activations extended into the mid-portion of the left middle/superior temporal cortex, a region implicated in retrieval of lexical and grammatical information about verbs (Crepaldi et al., 2011; Willms et al., 2011). While the conceptual and linguistic accounts cannot be teased apart in the context of our experiment (since verbs referred to actions and nouns referred to objects), studies investigating the nature of verb-related LOTC activations (Peelen et al., 2012; Bedny et al., 2014) confirm that whereas posterior lateral temporal regions store conceptual representations of actions, a distinct cluster in the left pMTG may be specialized for processing verbs as a grammatical class.

Recruitment of the left posterior parietal cortex is also sporadically reported during verb processing (Marangolo et al., 2006; Saccuman et al., 2006; Shapiro et al., 2006; Tsigka et al., 2014). While there is no consensus on the role of parietal regions in language tasks, recent studies suggest that they may be crucial for thematic role assignment (Thothathiri et al., 2012; Finocchiaro et al., 2015). On an alternative view, increased parietal activations during action naming may be explained by greater complexity of action drawings that for transitive verbs included not only agents, but also undergoers and instruments (Liljeström et al., 2008, 2009).

In addition, the searchlight analysis revealed that nouns and verbs showed significantly different activation patterns in virtually all left inferior frontal regions engaged in picture naming. The left IFG is traditionally associated with verb processing (for review, see Cappa and Perani, 2003), although it is a matter of debate whether its activation in the verb vs. noun contrast indicates the presence of verb-specific linguistic information in this area or is rather explained by morphosyntactic or task demands (Berlingeri et al., 2008; Siri et al., 2008; Vigliocco et al., 2011). The prefrontal cortex also mediates executive function, and in the context of our study activation differences between nouns and verbs in this area may reflect differences in lexical selection demands, as verbs have more synonyms/hyponyms/hyperonyms than nouns, and thus place more load on selection processes (Kan and Thompson-Schill, 2004).

Using MVPA, we were able to reliably decode nouns and verbs in posterior ventral occipitotemporal cortices bilaterally, consistent with the role attributed to this area in representation of object concepts (for review, see Martin, 2007). The univariate analysis detected only a small noun-preferring cluster in the left posterior fusiform, which may have to do with the fact that our stimuli were selected from a wide range of semantic categories whose conceptual representations are distributed along the ventral occipitotemporal cortex.

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Training-related activation decreases in left anterior regions

Training of nouns and verbs was associated with significant decreases of the BOLD response in the left IFG and anterior insula, replicating findings of studies on repeated object naming (van Turennout et al., 2000, 2003; Meister et al., 2005; Meltzer et al., 2009; Basso et al., 2013; MacDonald et al., 2015). Notably, activation decreases in these regions were significantly greater after the explicit training as compared to a single word repetition over the course of two weeks, attesting to the cumulative nature of practice.

Activation of the left posterior IFG during naming tasks has been ascribed to a number of linguistic functions, including both phonological and semantic processing (Poldrack et al., 1999; Vigneau et al., 2006). Although the practice-related decreases of the BOLD signal in this region may be attributed to facilitation at any level(s) of language processing, they may also be explained by decreased reliance on executive mechanisms, such as response selection and inhibition of competing responses (Thompson-Schill et al., 1997, 1999). Indeed, subjects were encouraged to settle on target words from the beginning and stick to them throughout the training. This may have increased name agreement, thus decreasing left prefrontal activation (Kan and Thompson-Schill, 2004).

Activation decreases in the left anterior insula support findings of Basso et al. (2013), who compared the BOLD responses to low-frequency nouns before and after training with response to high-frequency nouns that were not involved in practice. While prior to training low-frequency items yielded greater activations in the insula bilaterally, in the post-training session they were indistinguishable from high-frequency items. Hence, training effects in the left anterior insula may mimic frequency effects, as the usage frequency of trained items was manipulated by intensive repetition. Supporting evidence comes from previous studies implicating insula in processing of low-frequency words (Binder et al., 2005; de Zubicaray et al., 2005; Carreiras et al., 2006; Graves et al., 2007).

Training-related activation changes in left temporal and parietal regions

MVPA distinguished activation patterns associated with naming of trained and untrained words in several posterior regions of the left hemisphere, including the precuneus, angular gyrus and posterior superior temporal sulcus (pSTS).

As discussed above, posterior lateral temporal cortices are implicated in storage of conceptual and lexical representations. Specifically, activation in pSTS is often attributed to processing of lexical word forms (Indefrey and Levelt, 2004; Hickok and Poeppel, 2007). In our study, activation changes in this region might reflect facilitated access to phonological representations of the trained words. Interestingly, sparing of this region was the sole predictor of anomia recovery in a lesion-symptom mapping study (Fridriksson, 2010; Supplementary Figure 2, blue sphere), attesting to its role in word retrieval. Notably, as shown by diffusion-weighted imaging (DWI) studies in healthy subjects, posterior lateral temporal regions are extensively connected to the eloquent areas in the left IFG by the arcuate fasciculus, both directly and indirectly, via the inferior parietal lobule (Catani et al., 2005).

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Practice-related increase of the BOLD signal in the precuneus has been reported in several studies of repeated object naming in healthy populations (Basso et al., 2013; MacDonald et al., 2015; Kurland et al., 2018) and in patients with aphasia (Fridriksson et al., 2007; Fridriksson, 2010; Heath et al., 2015). Increased response of the precuneus and the angular gyrus was also reported following sentence repetition (Hasson et al., 2006; Poppenk et al., 2016). Kurland et al. (2018) documented practice effects following several repetitions of nouns and verbs in a portion of the inferior parietal lobule, closely overlapping with the angular gyrus cluster identified by our study (Supplementary Figure 2, yellow sphere). The above-mentioned studies linked activation of the parietal regions to the explicit memory of practiced items. Evidence consistent with this view was reported by Schott et al. (2005), who found that only conscious recognition of previously studied items (but not priming in the absence of explicit memory) yielded increased response in the precuneus and the inferior parietal lobule.

Whereas the role of precuneus in mediating episodic memory has been long established, the supporting role of the angular gyrus in this process was highlighted relatively recently (Yazar et al., 2012; Seghier, 2013). Importantly, fibers from the angular gyrus project both to the domain-general regions implicated in long-term memory, including the precuneus, and to the IFG (Seghier, 2013), which makes this area well-suited to mediate language learning.

Conclusions

While at first glance training-related changes outside of the classic language circuit may seem surprising, our results map well onto the studies in anomic patients that report a positive relationship between treatment-induced naming improvement and modulation of activity in the lateral and medial parietal cortices (Fridriksson et al., 2007; Menke et al., 2009; Fridriksson, 2010). Although functional changes in parietal regions did not receive much attention in the clinical literature (that mostly focuses on the perisylvian areas and their right-hemispheric homologues), they may support naming recovery in some patients with chronic aphasia. Thus, the intactness and potential functional reorganization of these areas following practice should be considered in naming treatment studies with patients.

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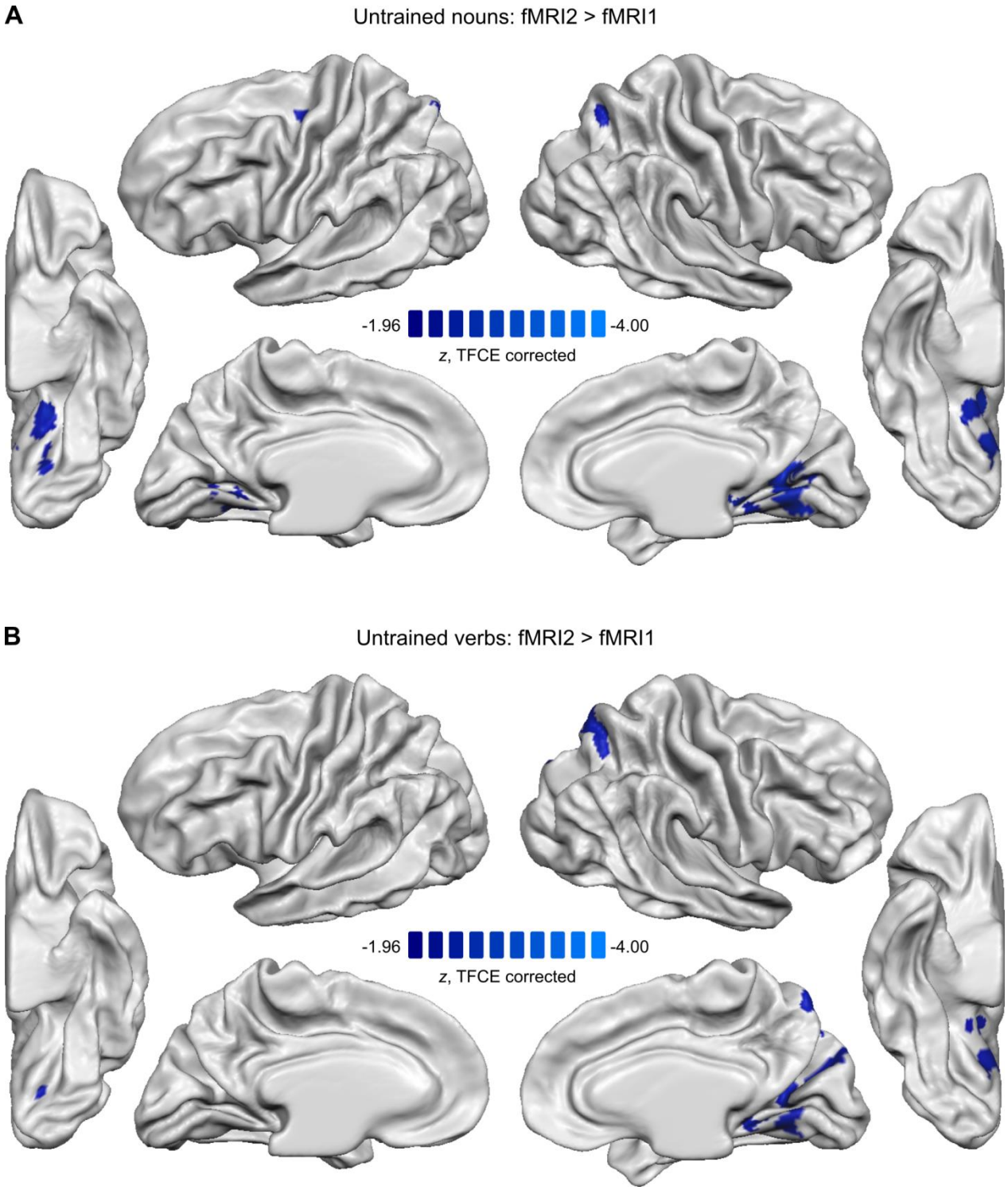
Supplementary Material



Supplementary Figure 1. Session effects, stemming from stimulus priming and/or task habituation, as revealed by the univariate contrasts of untrained nouns (*A*) and untrained verbs (*B*) across the two fMRI sessions. The statistical group map (N = 20) for each hemisphere was corrected for multiple comparisons using TFCE (α = .05, two-tailed) and projected onto the group-averaged surface meshes for visualization.

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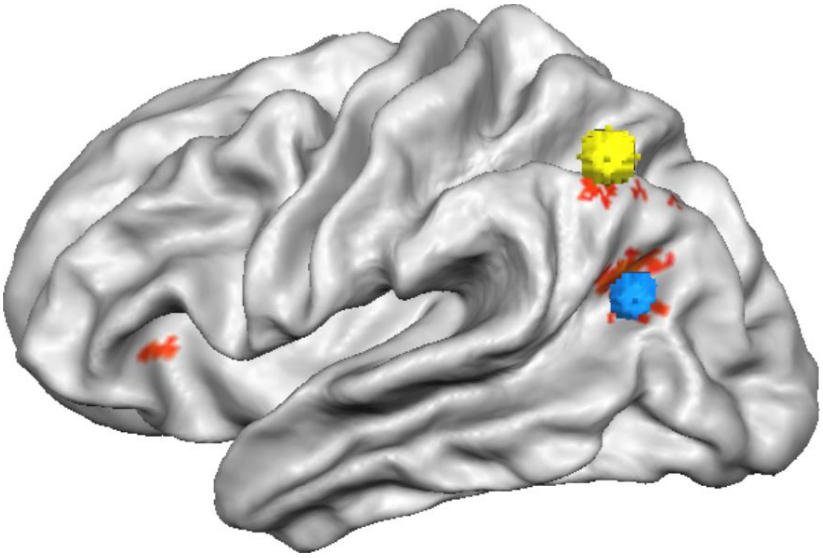

Supplementary Figure 2. Overlapping results of the multivariate analysis of training effects in our study (red clusters) with the areas identified in a lesion-mapping study of anomia treatment (Fridriksson, 2010; blue sphere, posterior temporal lobe, xyz_{TAL} = -36, -64, 18) and a naming practice study with healthy individuals (Kurland et al., 2018; yellow sphere, angular gyrus, xyz_{TAL} = -42, -59, 43). Spheres were created with a 5-mm radius around the coordinates reported in the corresponding studies. The coordinates were converted from the MNI to the Talairach space using the Yale BioImage Suite Package (http://www.bioimagesuite.org; RRID: SCR_002986).

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Supplementary Table 1. Object and action naming networks, as identified by the univariate contrasts of object/action drawings with phase-scrambled controls in the pre-training fMRI session. Information about the active clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; $z > 1.96$) back into the volume. The table shows average *z*-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding *z*-value and anatomical label. Local maxima are reported for clusters larger than 5000 mm^3. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			local maxima				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Objects > Scrambles in fMRI1							
LH	2.87	29590	3.09	-21	15	-10	Orbital gyrus
			3.09	-23	-6	-14	Parahippocampal gyrus
			3.09	-25	-40	-10	Fusiform gyrus
			3.09	-28	27	-3	Orbital gyrus
			3.09	-27	-76	22	Superior parietal lobule
			3.09	-35	-39	-15	Fusiform gyrus
			3.09	-30	-4	-24	Parahippocampal gyrus
			3.09	-39	21	12	Inferior frontal gyrus (frontal operculum)
			3.09	-32	-80	-13	Inferior occipital gyrus
			3.09	-34	-80	8	Middle occipital gyrus
			3.09	-37	-19	-19	Fusiform gyrus
			3.09	-39	-64	-9	Fusiform gyrus
			3.09	-38	5	32	Inferior frontal gyrus (pars opercularis)
			3.09	-39	-73	20	Middle occipital gyrus
			3.09	-42	-72	0	Inferior occipital gyrus
			3.09	-49	-56	-6	Middle temporal gyrus
LH	2.22	683	2.46	-7	-53	10	Precuneus
LH	2.09	719	2.17	-5	20	48	Superior frontal gyrus (pre-SMA)
RH	2.72	16800	3.09	43	-63	-4	Inferior occipital gyrus
			3.09	38	-60	-11	Fusiform gyrus
			3.09	35	-75	-10	Inferior occipital gyrus
			3.09	36	-77	10	Middle occipital gyrus
			3.09	32	-80	4	Middle occipital gyrus
			3.09	38	-40	-15	Fusiform gyrus
			3.09	28	-41	-12	Fusiform gyrus
			3.09	27	-86	-1	Middle occipital gyrus
			3.09	34	-19	-18	Parahippocampal gyrus
			3.09	28	-33	-17	Fusiform gyrus
			2.65	28	-2	-20	Parahippocampal gyrus
			2.51	27	25	-5	Orbital gyrus
RH	2.08	542	2.17	22	-74	30	Superior parietal lobule

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Actions > Scrambles in fMRI1							
LH	2.91	31331	3.09	-21	-74	33	Superior parietal lobule
			3.09	-26	-77	23	Superior parietal lobule
			3.09	-24	14	-9	Anterior insula
			3.09	-24	-6	-17	Parahippocampal gyrus
			3.09	-25	-36	-11	Fusiform gyrus
			3.09	-29	25	-3	Orbital gyrus
			3.09	-31	-21	-19	Parahippocampal gyrus
			3.09	-29	-86	-2	Middle occipital gyrus
			3.09	-34	-78	21	Middle occipital gyrus
			3.09	-37	-38	-15	Fusiform gyrus
			3.09	-39	23	16	Inferior frontal gyrus (frontal operculum)
			3.09	-41	-59	-9	Fusiform gyrus
			3.09	-38	3	32	Inferior frontal gyrus (pars opercularis)
			3.09	-40	-69	13	Middle temporal gyrus
			3.09	-41	-74	-2	Inferior occipital gyrus
			3.09	-46	15	19	Inferior frontal gyrus (pars triangularis)
			3.09	-50	-56	3	Middle temporal gyrus
LH	2.25	711	2.51	-6	20	48	Superior frontal gyrus (pre-SMA)
LH	2.20	565	2.37	-7	-53	10	Precuneus
RH	2.86	22670	3.09	43	-63	4	Middle temporal gyrus
			3.09	39	-75	10	Middle occipital gyrus
			3.09	39	-60	-11	Fusiform gyrus
			3.09	42	-46	-12	Fusiform gyrus
			3.09	35	-74	-11	Inferior occipital gyrus
			3.09	39	-15	-21	Fusiform gyrus
			3.09	32	-79	5	Middle occipital gyrus
			3.09	34	-36	-16	Fusiform gyrus
			3.09	30	-44	-13	Fusiform gyrus
			3.09	29	-75	22	Transverse occipital sulcus
			3.09	32	22	3	Anterior insula
			3.09	27	-86	-3	Middle occipital gyrus
			3.09	26	-32	-13	Parahippocampal gyrus
			3.09	26	-1	-16	Parahippocampal gyrus
			3.09	22	-76	31	Superior parietal lobule

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Supplementary Table 2. Word class effects, as identified by the univariate contrast of object and action drawings in the pre-training fMRI session. Information about the active clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; z > 1.96) back into the volume. The table shows average z-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding z-value and anatomical label. Local maxima are reported for clusters larger than 5000 mm^3. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			local maxima				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Actions > Objects in fMRI1							
LH	2.80	5871	3.09	-39	-74	11	Middle occipital gyrus
			3.09	-42	-54	12	Superior temporal sulcus
			3.09	-43	-74	-2	Inferior occipital gyrus
			3.09	-46	-55	8	Superior temporal sulcus
			3.09	-44	-65	12	Middle temporal gyrus
			3.09	-48	-62	2	Middle temporal gyrus
			3.09	-51	-46	8	Superior temporal sulcus
			3.09	-55	-55	0	Middle temporal gyrus
LH	2.18	1282	2.29	-31	-47	47	Superior parietal lobule
LH	2.15	806	2.29	-39	-46	-14	Fusiform gyrus
LH	2.04	160	2.12	-21	-83	30	Superior parietal lobule
LH	2.00	110	2.01	-48	-27	34	Intraparietal sulcus
LH	1.99	72	2.00	-25	-70	22	Superior parietal lobule
LH	1.99	15	2.00	-29	-53	36	Superior parietal lobule
LH	1.99	33	2.00	-55	-25	30	Intraparietal sulcus
RH	2.66	8200	3.09	50	-50	4	Middle temporal gyrus
			3.09	44	-62	-1	Middle temporal gyrus
			3.09	48	-51	10	Middle temporal gyrus
			3.09	42	-66	12	Middle occipital gyrus
			3.09	39	-75	10	Middle occipital gyrus
			3.09	42	-58	8	Middle temporal gyrus
			3.09	38	-55	-12	Fusiform gyrus
			3.09	42	-42	-13	Fusiform gyrus
			2.65	46	-43	14	Superior temporal sulcus
RH	1.97	54	1.98	26	-90	-7	Inferior occipital gyrus
Objects > Actions in fMRI1							
LH	2.17	498	2.46	-7	-82	-9	Fusiform gyrus

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Supplementary Table 3. Word class effects, as identified by the searchlight analysis aiming to decode objects vs. actions in the pre-training fMRI session. Information about the detected clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; $z > 1.96$) back into the volume. The table shows average *z*-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding *z*-value and anatomical label. Local maxima are reported for clusters larger than 5000 mm^3. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			local maxima				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Objects vs. Actions in fMRI1							
LH	2.77	53629	3.09	-5	-76	10	Cuneus
			3.09	-7	-79	2	Calcarine sulcus
			3.09	-7	-64	-2	Fusiform gyrus
			3.09	-10	-75	-10	Fusiform gyrus
			3.09	-11	-86	17	Cuneus
			3.09	-10	-69	28	Parieto-occipital sulcus
			3.09	-17	-52	-5	Fusiform gyrus
			3.09	-17	-82	-11	Fusiform gyrus
			3.09	-14	-75	38	Parieto-occipital sulcus
			3.09	-21	-77	27	Superior parietal lobule
			3.09	-26	-88	5	Middle occipital gyrus
			3.09	-23	-59	-10	Fusiform gyrus
			3.09	-26	-71	30	Superior parietal lobule
			3.09	-26	-63	44	Superior parietal lobule
			3.09	-29	-79	19	Superior occipital gyrus
			3.09	-33	-48	-14	Fusiform gyrus
			3.09	-29	-50	48	Superior parietal lobule
			3.09	-34	-74	-12	Fusiform gyrus
			3.09	-38	-39	-14	Fusiform gyrus
			3.09	-38	-70	26	Angular gyrus
			3.09	-40	-71	10	Middle occipital gyrus
			3.09	-43	-55	17	Superior temporal gyrus
			3.09	-40	-36	44	Superior parietal lobule
			3.09	-41	-68	-8	Inferior occipital gyrus
			3.09	-50	-53	-6	Middle temporal gyrus
			3.09	-47	-65	4	Middle temporal gyrus
			3.09	-51	-43	4	Middle temporal gyrus
			3.09	-52	-32	27	Supramarginal gyrus
			3.09	-52	-46	16	Supramarginal gyrus
			3.09	-56	-33	9	Superior temporal gyrus
			2.65	-8	-50	38	Precuneus
LH	2.25	6310	2.51	-42	17	22	Inferior frontal gyrus (pars triangularis)

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			2.51	-46	2	26	Precentral sulcus
			2.51	-49	-1	12	Inferior frontal gyrus (frontal operculum)
			2.46	-41	11	23	Inferior frontal gyrus (pars triangularis)
			2.46	-37	2	46	Middle frontal gyrus
			2.41	-47	-7	38	Precentral gyrus
LH	2.03	212	2.12	-38	16	36	Middle frontal gyrus
RH	2.82	44008	3.09	52	-37	7	Superior temporal sulcus
			3.09	48	-56	2	Middle temporal gyrus
			3.09	45	-43	-14	Inferior temporal gyrus
			3.09	44	-57	20	Middle temporal gyrus
			3.09	36	-52	-8	Fusiform gyrus
			3.09	38	-75	10	Middle occipital gyrus
			3.09	33	-60	-10	Fusiform gyrus
			3.09	35	-70	-11	Inferior occipital gyrus
			3.09	28	-63	38	Superior parietal lobule
			3.09	33	-80	2	Middle occipital gyrus
			3.09	26	-75	24	Superior parietal lobule
			3.09	28	-38	-14	Fusiform gyrus
			3.09	26	-78	-11	Inferior occipital gyrus
			3.09	20	-89	1	Middle occipital gyrus
			3.09	12	-83	4	Calcarine sulcus
			3.09	15	-74	31	Parieto-occipital sulcus
			3.09	10	-67	-4	Fusiform gyrus
			3.09	8	-82	13	Cuneus
			2.88	32	-41	46	Superior parietal lobule
			2.75	7	-58	29	Precuneus
RH	2.18	387	2.41	48	23	22	Inferior frontal gyrus (pars triangularis)
RH	2.04	15	2.12	53	27	15	Inferior frontal gyrus (pars triangularis)
RH	2.02	31	2.12	46	8	25	Inferior frontal gyrus (pars opercularis)

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Supplementary Table 4. Training effects, identified as the univariate contrasts of trained and untrained items in the post-training fMRI session. Information about the active clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; $z > 1.96$) back into the volume. The table shows average z-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding z-value and anatomical label. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			**local maxima**				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Trained Nouns > Untrained Nouns in fMRI2							
LH	-2.02	241	-2.10	-29	15	5	Anterior insula
LH	-2.02	821	-2.05	-45	11	17	Inferior frontal gyrus (pars opercularis)
Trained Verbs > Untrained Verbs in fMRI2							
LH	-2.46	2588	-2.88	-42	9	23	Inferior frontal gyrus (pars opercularis)
LH	-2.42	2419	-2.88	-35	23	5	Anterior insula

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Supplementary Table 5. Session effects, as identified by the univariate contrasts of untrained items in the post- vs. the pre- training session. Information about the active clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; $z > 1.96$) back into the volume. The table shows average z-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding z-value and anatomical label. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			**local maxima**				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Untrained Nouns in fMRI2 > Untrained Nouns in fMRI1							
LH	-2.09	962	-2.37	-16	-51	-4	Fusiform gyrus
LH	-2.05	203	-2.14	-17	-68	-8	Fusiform gyrus
LH	-2.04	98	-2.10	-22	-14	50	Superior frontal sulcus
LH	-1.99	51	-2.01	-20	-62	3	Calcarine sulcus
LH	-2.01	142	-2.01	-17	-70	48	Superior parietal lobule
LH	-1.98	29	-2.00	-4	-62	2	Fusiform gyrus
RH	-2.16	3442	-2.26	12	-55	4	Calcarine sulcus
RH	-2.07	211	-2.14	19	-62	48	Superior parietal lobule
Untrained Verbs in fMRI2 > Untrained Verbs in fMRI1							
LH	-2.04	68	-2.07	-15	-72	-8	Fusiform gyrus
RH	-2.08	889	-2.14	14	-65	49	Superior parietal lobule
RH	-2.04	2380	-2.12	12	-59	8	Calcarine sulcus
RH	-1.98	108	-2.01	15	-71	40	Superior parietal lobule

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Supplementary Table 6. The compound univariate contrasts of across-session training vs. session effects, separately for nouns and for verbs. Information about the active clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, one-tailed; $z > 1.65$) back into the volume. The table shows average z-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding z-value and anatomical label. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			**local maxima**				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Training effects > Session effects for Nouns							
LH	-1.68	86	-1.71	-46	13	11	Inferior frontal gyrus (frontal operculum)
LH	-1.67	87	-1.70	-43	15	25	Inferior frontal gyrus (pars triangularis)
LH	-1.66	7	-1.68	-49	12	20	Inferior frontal gyrus (pars triangularis)
Training effects > Session effects for Verbs							
LH	-1.89	1222	-2.26	-40	8	26	Inferior frontal gyrus (pars opercularis)
LH	-1.85	772	-2.05	-29	16	3	Anterior insula
LH	-1.79	444	-1.98	-43	33	8	Inferior frontal gyrus (pars orbitalis)

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Supplementary Table 7. Training effects, as identified by the searchlight analysis aiming to decode trained vs. untrained items (collapsed across word classes) in the post-training fMRI session. Information about the detected clusters was obtained using NeuroElf, after projecting the thresholded statistical maps (corrected α = .05, two-tailed; $z > 1.96$) back into the volume. The table shows average *z*-values and extent (in mm^3) of active clusters, as well as the Talairach coordinates of each cluster's center-of-gravity (COG), its corresponding *z*-value and anatomical label. Clusters with the extent lesser than 10 mm^3 are not reported. LH = left hemisphere, RH = right hemisphere.

cluster			**local maxima**				
side	**mean *Z***	**mm^3**	***Z***	x_{COG}	y_{COG}	z_{COG}	**anatomical region**
Trained vs. Untrained items in fMRI2							
LH	2.38	489	3.09	-39	-63	20	Superior temporal sulcus
LH	2.31	98	2.58	-4	-65	28	Precuneus
LH	2.31	84	2.58	-28	24	5	Anterior insula
LH	2.26	139	2.51	-43	-57	39	Angular gyrus
LH	2.16	67	2.29	-28	-75	26	Angular gyrus
LH	2.18	22	2.29	-36	-61	40	Angular gyrus
LH	2.12	29	2.29	-41	-64	37	Angular gyrus
LH	2.14	30	2.26	-36	-71	36	Angular gyrus
LH	2.11	11	2.23	-7	-68	23	Precuneus
RH	2.15	44	2.33	3	-77	-6	Fusiform gyrus