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Rapid Cortical Plasticity Induced by Active Learning of Novel Words in Human Adults

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Abstract

Whether short-term learning of new words can induce rapid changes in cortical areas involved in distributed neural representation of the lexicon is a hotly debated topic. To answer this question, we examined magnetoencephalographic phase-locked responses elicited in the cerebral cortex by passive presentation of eight novel pseudowords before and immediately after an operant conditioning task. This procedure forced participants to perform an active search for unique meaning of four word-forms that referred to movements of their own body parts. While familiarization with novel word-forms led to bilateral repetition suppression of cortical responses to all eight pseudowords, these reduced responses became more selectively tuned towards newly learned action words in the left hemisphere. Our results suggest that stimulus repetition and active learning of semantic association have separable effects on cortical activity. They also evidence rapid plastic changes in cortical representations of meaningful auditory word-forms after active learning.

Keywords

associative learning, word semantics, MEG, repetition suppression, cortical plasticity, familiarization.

Introduction

Words are distinct, meaningful elements of any human language. Recognition of spoken words requires the brain to have invariant Gestalt-like phonological representations of complex auditory patterns that represent each known word (DeWitt & Rauschecker, 2012; Griffiths & Warren, 2004). On the other hand, word referential meaning allows us to use language as an information transfer carrier for inter-subject communication (Fodor, 1983). However, it remains poorly understood how these two tightly interconnected lexicality aspects become embodied in brain networks during acquisition of new items into a subject's lexicon.

The learning-induced changes in cortical responses elicited by conversion of a pseudoword into the real word is a subject of intense debate in the literature. The dual-learning system theory (Davis & Gaskell, 2009), based on functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) evidence, posits that formation of a new word representation, similarly to formation of other long-term memory traces, is a two-stage process (Davis & Gaskell, 2009; Gaskell & Dumay, 2003; Rodríguez-Fornells, Cunillera, Mestres-Missé, & de Diego-Balaguer, 2009). Initially, it involves rapid but short-lived learning of the new word, mainly subserved by the medial temporal memory system without substantial involvement of neocortical activity. The slowly emerging plastic changes in neocortical responses occur through off-line consolidation, i.e., strengthening of word representation within neocortical networks, and presumably develop during a night of sleep. Yet, in recent years, this theory has been challenged by research that suggests the involvement of the so-called "fast mapping" mechanism that converts pseudoword-related cortical activity into word-like responses after a short (tens of minutes) period of familiarization (Borovsky, Kutas, & Elman, 2010; Kimppa, Kujala, Leminen, Vainio, & Shtyrov, 2015; Mestres-Missé, Rodriguez-Fornells, & Münte, 2007; Sharon, Moscovitch, & Gilboa, 2011; Shtyrov, Nikulin, & Pulvermuller, 2010). The latter studies mainly used electromagnetic cortical event-related responses (ERP), which, unlike responses captured by fMRI and PET signals, reflect synchronized activity of cortical neurons precisely phase-locked to the onset of an external event.

The majority of the available electroencephalographic/magnetoencephalographic (EEG/MEG) studies sought evidence for fast and automatic formation of a phonological word-form cortical representation that results from repetitive presentation of pseudowords, while the subject's attention was directed elsewhere. Such data demonstrated that while the cortical response to pseudowords is initially weaker than that to real words, after a number of repetitions this difference is diminished (Kimppa et al., 2015; Shtyrov, 2011; Shtyrov et al., 2010). This phenomenon occurs due to opposite signs of repetition dynamics for real words and pseudowords. While cortical responses evoked by real words weaken with repetition, those for novel word-forms exhibit repetition enhancement. The authors suggest that their findings reflect the fast and automatic formation of memory traces for previously unfamiliar word-forms during passive listening. This view is further supported by mismatch-negativity (MMN) results (Shtyrov et al., 2010; Yue, Bastiaanse, & Alter, 2014). The researchers reported that pseudowords used as rare deviants started to evoke MMN of increased amplitude when presented late in the course of a passive exposure session compared with the early trials, while no such temporal dynamics was observed for real-word deviants. These MMN findings imply that phonological discrimination of a newly presented word-form is boosted after a short passive learning session that comprises approximately 150 repetitions of the same item for several minutes.

The above results were interpreted as an evidence that the adult brain can learn novel pseudowords in the course of passive listening without any cognitive or attentional effort; this process was supposed to result in the formation of "empty" lexical entries, treated by the brain as part of the lexicon that bear no meaning. However, the same results could be alternatively explained by more general biological mechanisms of perceptual learning (Seitz & Dinse, 2007). A mere familiarization with unattended stimuli leads to their improved discrimination, even when complex visual stimuli, such as natural or abstract images, are used in the discrimination task (Sasaki, Nanez, & Watanabe, 2010). This form of recognition memory for individual items can be accomplished by familiarity processing in extra-hippocampal regions of the medial temporal memory system (Bird, 2017; Brown & Aggleton, 2001).

Therefore, the opposite effects that passive repetition of pseudowords and real words exert on neural activity might result from their unbalanced perceptual history in the past experience. Indeed, familiarization that occurs for completely unfamiliar novel word-forms (but not for over-learned real word-forms) might involve implicit perceptual learning of pseudowords, which is not necessarily related to their inclusion in the lexicon.

Essentially, the above EEG/MEG studies of “fast mapping” addressed putative cortical plasticity related only to the phonological aspect of lexicality; a semantic aspect was beyond their scope. Meanwhile, the most popular approach in fMRI research that pursues cortical response transformation caused by acquired semantic meaning is associative learning (Rodríguez-Fornells et al., 2009). Such experiments contrast cortical activation alterations induced by passive presentation of two pseudoword types before and after an associative learning procedure. Since consistent association might potentially affect both phonological and semantic aspects of lexicality, cortical changes, to be considered as truly “semantic”, are assumed to occur in the higher-tier cortical areas that underlie semantic processing of real words. Such changes are in fact observed in these regions after consolidation (Davis & Gaskell, 2009).

To the best of our knowledge, there are only two EEG studies dedicated to associative learning of novel auditory words. In one of them (Fargier et al., 2014), ERPs to passive pseudoword presentation before and after learning were compared for pseudowords associated during learning either with short movies of reaching-and-grasping movements or with abstract visual images. As a result of learning, ERP started to differentiate both types of pseudowords within 100-400 ms after stimulus onset. In line with fMRI findings, reliable learning-induced changes in ERP occurred only on the second day after learning, supposedly after night-sleep consolidation. Thus, this ERP study provided little to no confirmation for semantic “fast mapping” in word learning.

The other available EEG study (François, Cunillera, Garcia, Laine, & Rodríguez-Fornells, 2017) explored efficacy of associative learning in comparison with statistical learning when the participants learned four tri-syllabic pseudowords presented within a continuous stream of auditory consonant-vowel (CV) syllables. The results showed that during the learning phase, the “semantic” N400 component of the ERP (Kutas & Federmeier, 2011) is elicited by pseudowords associated with visual images but not by pseudowords detected solely on the probability of transitions between syllables embedded into a continuous auditory stream. However, these ERP findings did not provide evidence for the “fast mapping” hypothesis. Indeed, since the participants were required to listen carefully to the auditory stream with the task of discovering new words, learning-related enhancement of N400 might have been elicited by an on-line attentional modulation, i.e., attention biased toward auditory word-forms associated with pictures during the learning session.

To prove semantic cortical plasticity, enhanced N400 should be observed during passive exposure to the newly learned word-forms.

In summary, the current picture of "fast mapping" in word learning is obviously far from complete. It is a controversial topic with a body of associated literature, yet the mere existence of "fast mapping" in forming cortical representations of word semantics is still considered doubtful by many (see Cooper, Greve, Henson, Greve, & Henson, 2018 for review). One of the reasons for this skepticism might be the passive nature of the learning procedure used in the previous experiments. A word, which is learned passively through repetition or instructions, is typically not well retained or effectively used. Active search for word meaning might be a preferred mode for inducing fast semantic mapping. Indeed, animal data suggest that the most effective way to induce cortical plasticity in adult primates is the operant conditioning paradigm. For example, a series of studies by Blake and colleagues (Blake, Heiser, Caywood, & Merzenich, 2006; Blake, Strata, Churchland, & Merzenich, 2002; Blake, Strata, Kempter, & Merzenich, 2005) showed that a fast and permanent transformation in cortical neuronal activity occurs in primates only if an active operant conditioning procedure is used (and not through passive stimulus-reward associative pairing).

In the current MEG study, which employed an operant conditioning task, we sought evidence for putative cortical "fast mapping" of two interactive but separate processes: formation of a new acoustic word-form discrimination and semantic analysis of the newly-formed coherent item. To pursue this goal, we engaged our participants in the pseudoword-action associative learning task to let them actively find unique associations between four auditory pseudowords and their own body part movements, whereas the other four auditory pseudowords were not supposed to be associated with any motor action. To reveal the learning effect on word-form-related and semantic-related cortical activity, we compared responses to passive presentations of the two pseudoword types before and after learning sessions. We used the MEG neuroimaging technique, which offers the best combination of excellent time resolution and good spatial resolution, factors that allowed us to identify the anticipated effects both in terms of their timing and the involved cortical regions.

Results

During the experiment, participants were presented with eight pseudowords (*Table 1*; *Figure 1*). The active task performed by participants was to learn specific associations between action pseudowords (APW) and motor actions by their hands and feet, while refraining from any responses to non-action pseudowords (NPW; *Table 1*). MEG was recorded during 'Passive block 1', which preceded word-form learning, and during 'Passive block 2', which followed learning (*Figure 1B*).

Table 1. Stimulus-to-response mapping.

APW			**NPW**		
Pseudoword	**Pronunciation**	**Assigned action**	**Pseudoword**	**Pronunciation**	**Assigned action**
hicha	[xʲˈi t͡ɕə]	left hand	*hichu*	[xʲˈi t͡ɕʊ]	none
hishu	[xʲˈiʂʊ]	left foot	*hisha*	[xʲˈiʂə]	none
hisa	[xʲˈis̪ə]	right foot	*hisu*	[xʲˈis̪ʊ]	none
hivu	[xʲˈivʊ]	right hand	*hiva*	[xʲˈivə]	none

Stimulus types: APW - action pseudoword; NPW - non-action pseudoword.

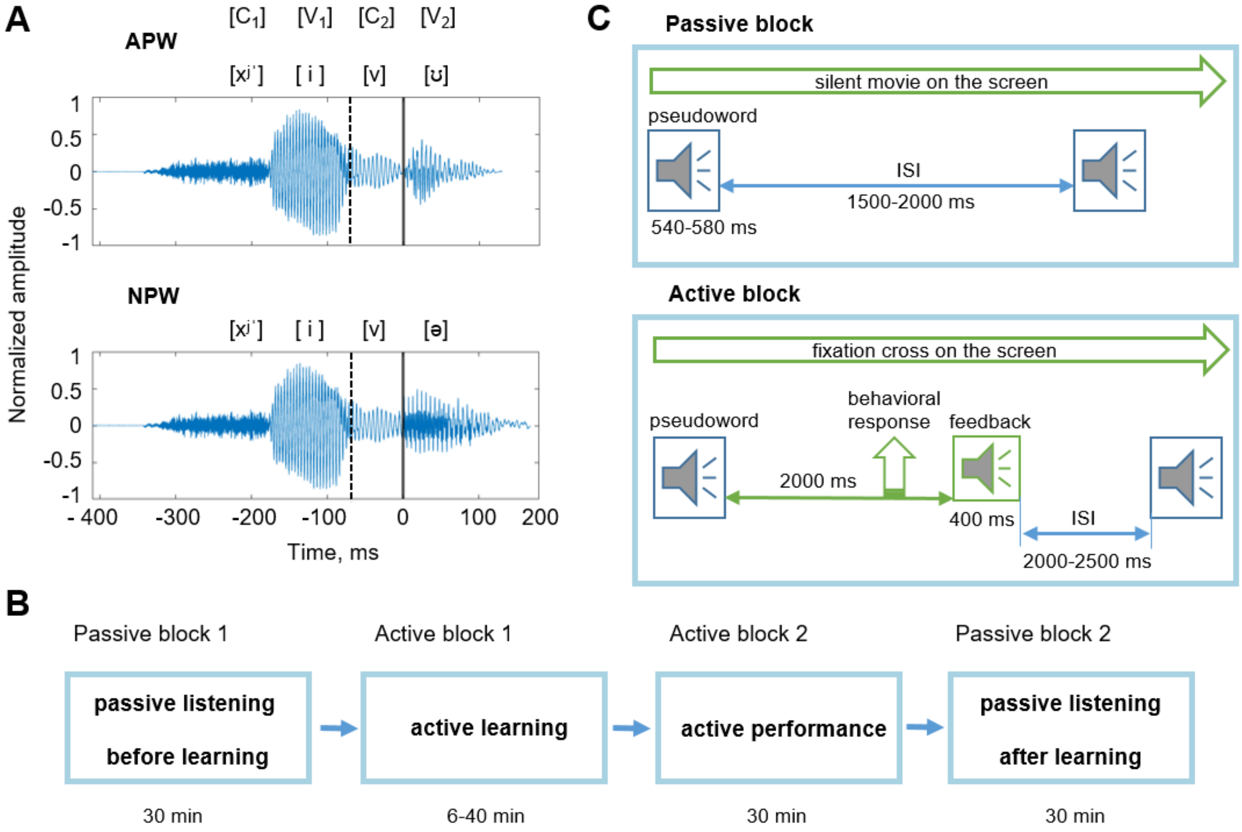

Figure 1. Stimuli and experimental design. **(A)** Examples of pseudoword stimuli: ‘hivu’ and ‘hiva’. All stimuli were two-syllable pseudowords ($C_1V_1C_2V_2$). The first syllable C_1V_1 (‘hi’) was the same for all pseudowords. Pseudowords were organized in pairs; each pair differed from the other pairs by the third phoneme, the consonant C_2. Each pair included an action pseudoword (APW) and a non-action pseudoword (NPW), which differed from each other in the last vowel V_2 (either ‘a’ or ‘u’; Table 1). Here and hereafter, a zero value on a timeline and a vertical solid line denote the onset of the fourth phoneme (word-form uniqueness point [UP]); a vertical dashed line indicates the onset of the third phoneme. **(B)** The sequence of experimental blocks. **(C)** The experimental procedure during passive blocks (upper panel) and active blocks (bottom panel); ISI refers to the interstimulus interval. During both passive blocks, participants were offered to watch a silent movie while auditory stimuli were presented. During active blocks, participants learned associations between pseudowords and motor actions.

First, we examined possible general neural mechanisms related to deep familiarization with pseudoword word-forms regardless of whether they were selectively associated with a referential action. We hypothesized that there is a common time window, during which changes in brain activity caused by word-form familiarization can be observed both for pseudowords that acquire a unique association with a specific movement (APW) and for those that do not (NPW). We expected to see these changes reflected in the phase-locked cortical responses starting 100–200 ms after pseudo-word onset in the perisylvian speech areas, which are thought to be engaged in the phonological processing of an auditory word (DeWitt & Rauschecker, 2012). Secondly, we explored the cortical plasticity signature in the semantic brain network. To this end, we anticipated finding modulation of cortical activity by learning at a later time (300-500 ms) in the higher-tier speech areas in the temporal and frontal cortices that mediate semantic analysis of word-forms (Kutas & Federmeier, 2011). Critical for our hypothesis, we predicted that the latter "semantic" modulation would be observed selectively for the meaning-related pseudowords (APW) and would be absent for the well-familiarized but meaningless word-forms (NPW). In contrast to the previous EEG/MEG "fast mapping" studies, we did not focus our analysis on the pre-specified cortical regions or the time intervals of cortical responses, and we employed an unbiased data-driven search (with correction for multiple comparisons) to reveal when and where in the cortex learning of novel word-forms and/or acquiring their semantics would induce neural activity changes.

Behavioral performance

All participants were successful with the task: average accuracy during the active performance block was 95.2 ± 5.8% (mean [M] ± standard deviation [SD], APW and NPW trials pooled together). Average d' was 5.4 ± 1.1 (M ± SD). The total number of errors committed by participants during the active performance block was between 0 and 21 out of 320 trials.

Familiarization effects (sensor-level analysis)

Figure 2A shows the root mean square (RMS) waveforms, calculated across gradiometers within left- and right-hemispheric regions of interest (ROIs), for passive presentation of APW and NPW in "before learning" and "after learning" conditions. These data illustrate the time courses of the overall signal strength of event-related fields (ERFs).

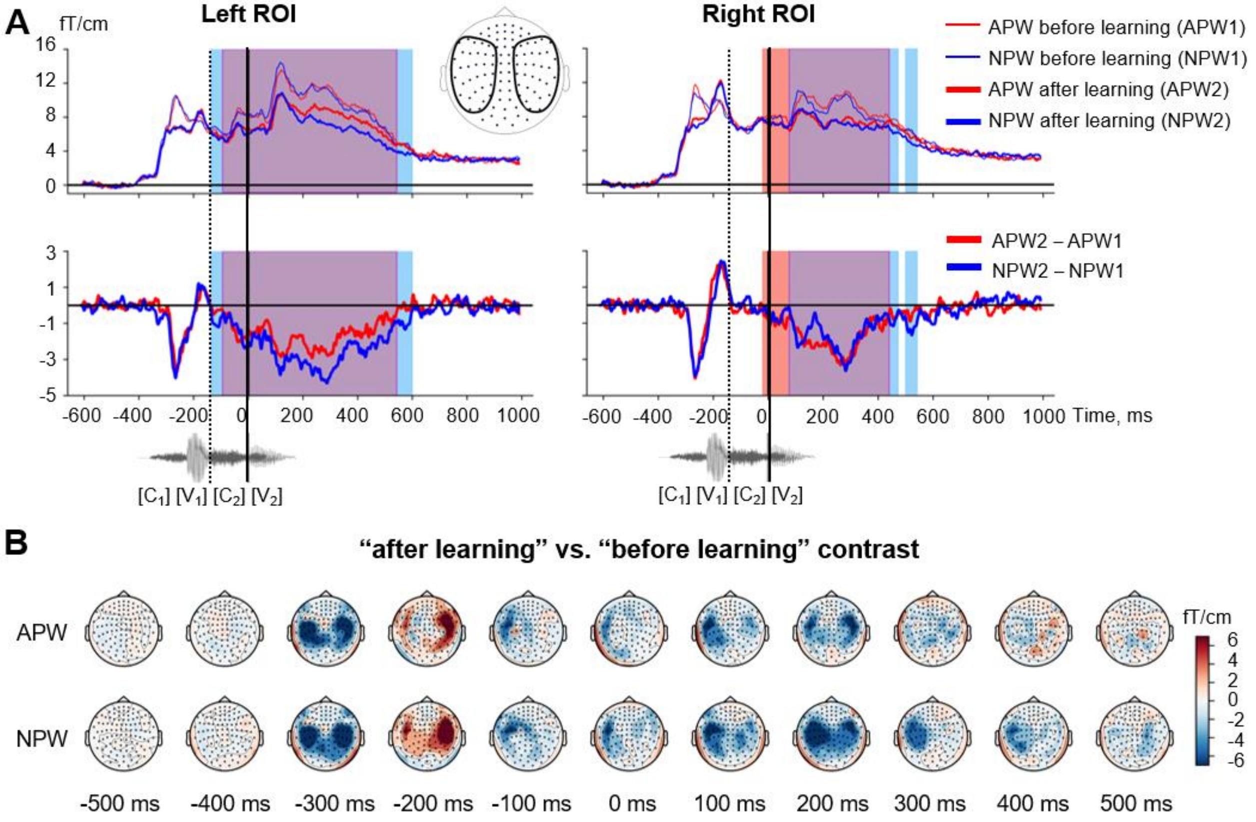

Figure 2. Repetition suppression effect in the sensor-space. **(A)** Time courses of the grand-average RMS signals. *Upper panel:* RMS time courses averaged over left and right ROIs (see insert) under passive listening to APW (red) and NPW (blue) stimuli presented before learning (thin red and blue lines) and after learning (thicker red and blue lines). *Bottom panel*: difference in RMS time courses between two passive listening blocks (APW2-APW1 and NPW2-NPW1, thick red and blue lines, respectively). A significant repetition suppression effect for APW and NPW is shown as the blue and pink shaded areas in RMS plots of APW and NPW trials, respectively; the purple shaded area corresponds to the temporal overlap of two effects (threshold-free cluster enhancement [TFCE] permutation statistics for “after learning” versus “before learning” contrasts). The waveform of the example stimulus ‘hiva’ aligned with the RMS timeline is shown at the bottom. Zero value on a timeline and a vertical solid line denote the onset of the fourth phoneme (word-form UP); a vertical dashed line shows the onset of the third phoneme. **(B)** Grand average topographic maps of the repetition effect magnitude for APW and NPW stimuli (APW2-APW1 and NPW2-NPW1 in the upper and bottom rows, respectively). Topographic maps are plotted in 100 ms steps; time is shown relative to the UP.

Passive repetition of both stimulus types after learning led to a short-lived reduction in the amplitude of the M100 ERF component in both left- and right-hemispheric ROIs, and, most probably, was related to familiarization with the first phoneme of the stimuli. Although, according to the threshold-free cluster enhancement (TFCE)-based permutation statistical procedure (see below) this transient effect was not significant, it was significant in both ROIs when we applied a less conservative uncorrected paired T-test to the changes in the M100 peak values (T(23) = 3.52, p = 0.002 and T(23) = 4.62, p = 0.0001 for the left and the right ROIs, respectively). Another short-lived repetition effect of the opposite sign arose approximately 100 ms later and was related to the right-hemispheric M200 component of the auditory ERF. The M200 repetition enhancement was significant for the right ROI only, specifically when tested at the time points that corresponded to the peak of the respective deflection (T(23) = -1.56, p > 0.1 and T(23) = -3.19, p = 0.004 for the left and the right ROIs, respectively), but once again it was not confirmed by the TFCE-based permutation statistical procedure (see below). Nevertheless, a similar increase in the magnitude of the right-hemispheric ERP component P200 through repetition of the rule-based constructed auditory pseudowords was reported in the previous word learning studies (Balaguer et al., 2007; Rodríguez-Fornells et al., 2009). The authors argued that the P200 repetition enhancement effect in their experimental settings reflected a build-up of attentional engagement by salient cues that required selection of relevant information, and this proposed interpretation is concordant with our current M200 findings. Topographical ERF maps showed that both early transient repetition-sensitive effects were similar for APW and NPW (*Figure 2B*). Considering the lack of an *a priori* hypothesis regarding these early effects and their rather weak statistical reliability, we did not proceed with their further analysis.

Our hypothesis was focused on repetition effects at later latencies that were related to the time when different auditory pseudowords started to be discriminable from each other as coherent word-forms, i.e., around and after the uniqueness point (UP). To this end, TFCE-based permutational statistical analysis revealed significant long-lived neural activity attenuation during the second passive block compared with the first one, and this modulation affected responses to both APW and NPW stimuli. For the ERF data collapsed across APW and NPW trials, response suppression lasted from approximately -135 ms to 595 ms relative to the UP in the left ROI and from -20 ms to 550 ms in the right ROI. As seen in *Figure 2A*, the time intervals of significant suppression for APW and NPW calculated separately substantially overlapped.

Topographical maps (*Figure 2B*) demonstrated that this prolonged effect started approximately 100 ms before the UP, reached its maximum 200 ms after the UP, and continued during the subsequent 300 ms (while gradually fading). Thus, the second passive presentation of the same word-forms led to a bilateral neural response attenuation to the temporal combination of the successive phonemes for both APW and NPW stimuli. A relatively early onset along the RMS time course suggests that the response attenuation was likely linked to the onset of the third rather than the fourth phoneme during auditory word-form processing.

Familiarization effects (source-level analysis)

To identify cortical areas that contributed to neural repetition suppression resulting from familiarization with the novel pseudowords, we analyzed the data in the source-space. As described in Methods, we evaluated cortical clusters that underwent significant suppression across the whole-time interval, as revealed by the RMS analysis. Significant neural activity suppression ($q < 0.05$; false discovery rate [FDR]-corrected) occurred in a wide network of cortical areas (*see Figure 3 and Figure 3 - Supplementary Figure A*).

To allow comparison of our results with the previous findings on repetition-sensitive effects in word learning (Kimppa et al., 2015; Macgregor, Pulvermüller, Casteren, & Shtyrov, 2012; Shtyrov, 2011; Shtyrov et al., 2010), we examined two consecutive time periods: the earlier (50-150 ms after the UP) and later (150-400 ms after the UP) ones. The source-space analysis performed separately for these periods showed that significant neural activity suppression ($q < 0.05$; false discovery rate [FDR]-corrected) occurred within both time periods and affected widely distributed cortical areas in both hemispheres, including the lateral and opercular surface of the temporal lobe, insula, lateral and ventral parts of the motor cortex, and inferior parietal regions (*Figure 3*; see also *Figure 3 - Supplementary Figure B* for depiction of the same analysis performed separately for APW and NPW conditions).

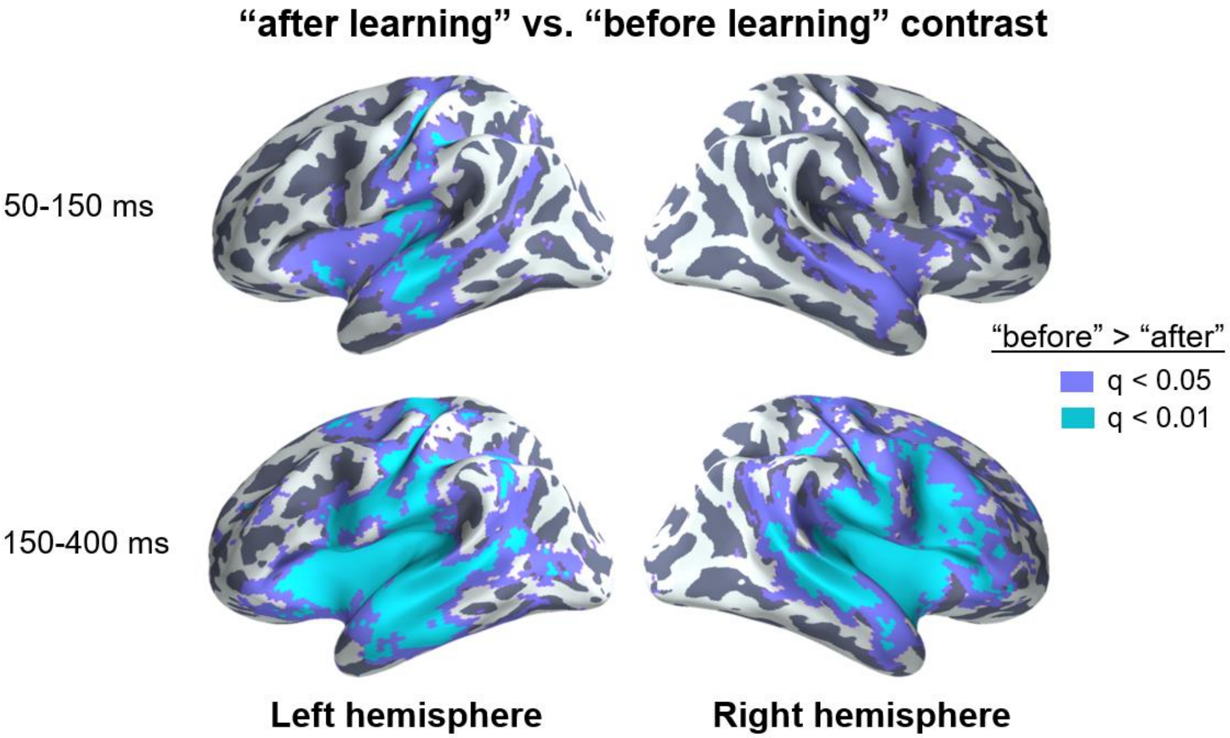

Figure 3. The repetition suppression effect in the source-space. Statistically thresholded maps (voxel-wise paired T-test, FDR-corrected, $q < 0.05$ and $q < 0.01$, are shown in purple and light-blue colors, respectively) for "after learning" versus "before learning" contrasts. The results are represented for two time windows: early (50-150 ms after the UP) and late (150-400 ms; see also *Figure 3 - Supplementary Figure A*). For this analysis, the APW and the NPW trials were pooled together (see also *Figure 3 - Supplementary Figure B* for APW and NPW stimuli analyzed separately).

Semantic learning effects (sensor-level analysis)

To unravel the putative effect of association learning, we analyzed the differences in the neural responses between APW and NPW "after leaning" (APW2 – NPW2) versus "before learning" (APW1 – NPW1) during passive blocks (*Figure 4*). Both RMS signal timecourses (*Figure 4A*) and ERF topographical maps (*Figure 4B*) demonstrated that whereas cortical activity evoked by the two pseudoword types did not differ before learning, the strength of differential neural responses to APW significantly increased after the learning procedure in the left ROI.

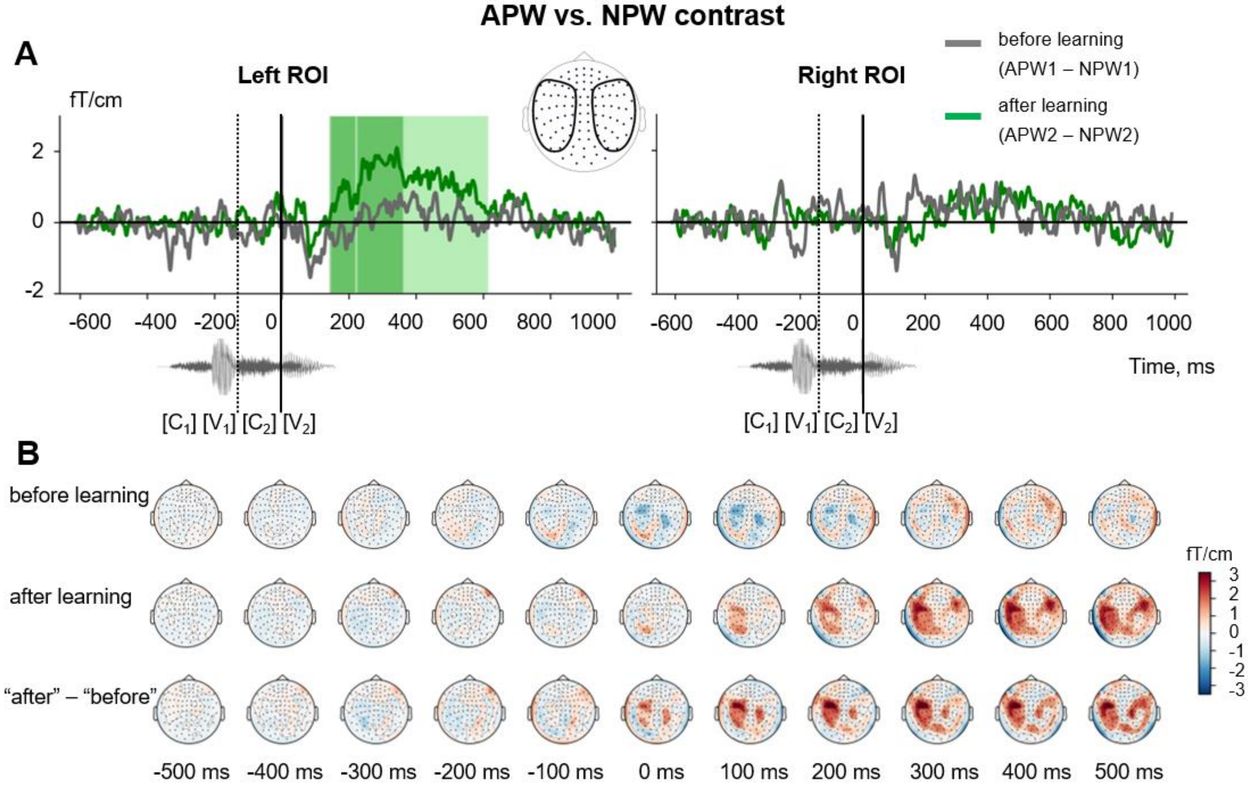

Figure 4. The associative learning effect in the sensor-space. **(A)** Grand average differential RMS time courses for APW versus NPW contrast "before learning" (APW1 – NPW1, grey) and "after learning" (APW2 – NPW2, green). The light green shaded area marks the time interval in "after learning" neural responses that correspond to a significant APW2 > NPW2 contrast according to TFCE permutation statistics. The shaded dark green areas designate the time intervals for a significant learning effect ([APW2 – NPW2] > [APW1 – NPW1]). A zero value on a timeline and a vertical solid line denote the onset of the fourth phoneme in the auditory pseudowords (word-form UP); a vertical dashed line shows the onset of the third phoneme. **(B)** Grand average topographic maps of differential ERF for APW versus NPW contrast "before learning" (APW1 – NPW1, top row) and "after learning" (APW2 – NPW2, middle row). The bottom row represents the associative learning effect: "after leaning" minus "before learning" ([APW2 – NPW2] > [APW1 – NPW1]). Topographic maps are plotted in 100 ms steps; time is shown relative to the UP.

The responses showed greater selectivity for the APW for the protracted response time interval that started approximately 150 ms after the onset of the fourth phoneme, which distinguished APW from NPW stimuli. TFCE-based permutational statistical analysis of the differential RMS signals produced two statistically significant intervals for the associative learning effect in the left ROI: 144-217 ms and 226-362 ms after the UP. To ensure that the APW-NPW difference in the neural responses before and after learning did result from learning, we additionally checked for the significance of the APW-NPW difference separately for the two conditions (“before learning” and “after learning”) using the same TFCE permutation statistical procedure. Neural responses following APW and NPW trials started to statistically discriminate the two types of pseudowords only after learning (significant from 145 to 615 ms), without any significant differences detected before learning (*Figure 4*).

Remarkably, unlike familiarization-related changes in the neural response, the semantic-sensitive transformation of cortical activity was bound to the moment in time when the two pseudoword types started to be recognizable by the brain. Given the narrow gap that separates the two temporal clusters, for source-space analysis we joined them and further considered the 150-400 ms interval after the UP.

Semantic learning effects (source-space analysis)

Since the sensor-level results revealed the semantic learning effect only in the left ROI and at the specific time interval, the following source reconstruction was restricted to the left hemispheric cortical responses within the 150-400 ms interval after the UP. For each of the four conditions, the source strength was averaged across the above interval before the statistical comparisons.

Figure 5 (*right panel*) demonstrates the after-learning enhancement in the activation strength of cortical sources in response to APW compared with NPW within “before learning” and “after learning” conditions (passive blocks 1 and 2 correspondingly). The largest contribution to the effect was from anterior parts of the superior temporal sulcus (aSTS)/middle temporal gyrus (MTG), insula/frontal operculum, triangular portion of inferior frontal gyrus (IFG), and the orbital area of prefrontal cortex. During the earlier 50-150 ms post-UP interval, virtually no identifiable activation changes caused by learning can be seen (*Figure 5, left panel*).

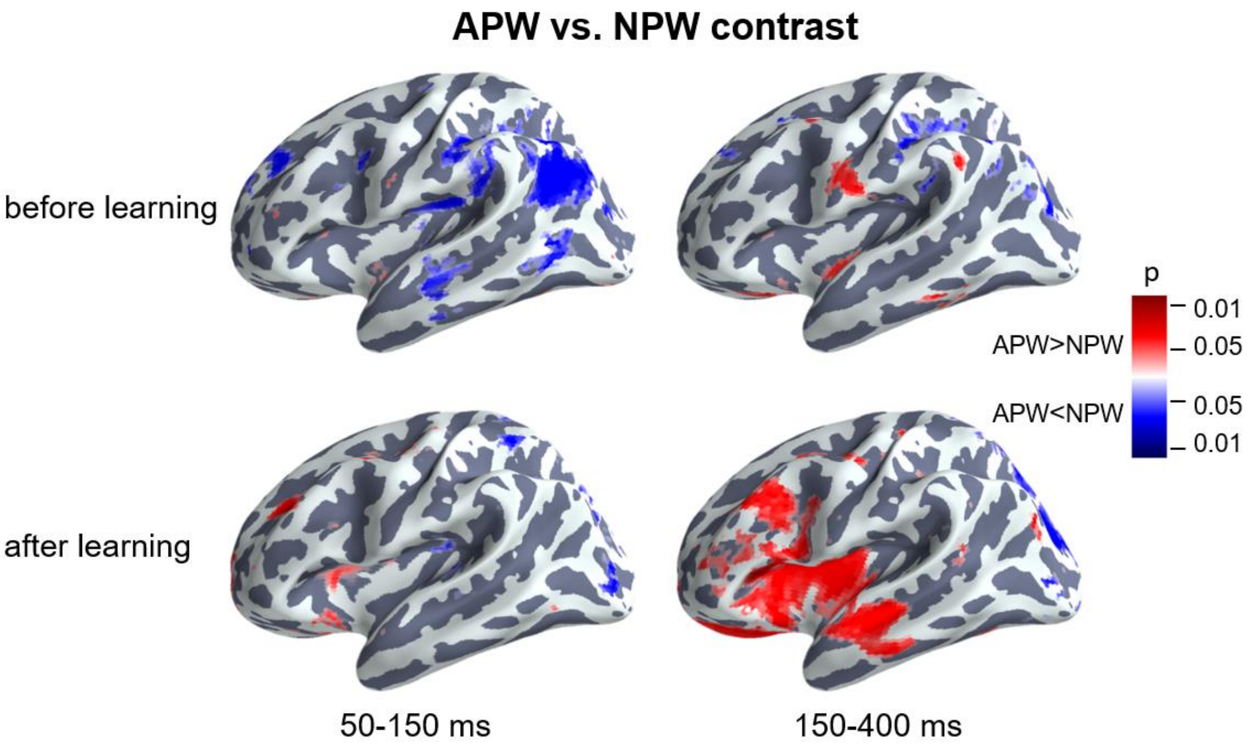

Figure 5. Cortical areas engaged in the associative learning effect (source space analysis). Statistically thresholded cortical topography for the APW versus NPW differential neural responses “before learning” (APW1 - NPW1, top row) and “after learning” (APW2 - NPW2, bottom row) (voxel-wise paired T-test, $p < 0.05$, uncorrected). The 150-400 ms time interval corresponds to the significant learning effect on APW versus NPW contrast according to the RMS data, which survived after correction for multiple comparisons (right column). The 50-150 ms time interval (left column) is presented for the sake of comparison with previous studies. The color scale represents p-values; color denotes the sign of the effect: red for APW > NPW and blue for APW < NPW.

To further explore the temporal dynamics of the semantic learning effect, we reconstructed the cortical sources that corresponded to the statistical significance maxima of the differential effect along the RMS timecourse: 190, 265, and 325 ms after the UP. Activations at cortical vertices were averaged over 35 ms intervals centered around each maximum, and cortical clusters that contained more than 20 adjacent vertices with the supra-threshold semantic learning effect (“after leaning” [APW2 – NPW2] versus “before learning” [APW1 – NPW1]; $p < 0.05$, uncorrected) were considered further (see *Table 2* for the list of the respective clusters). *Figure 6* shows the cortical location of the clusters reconstructed at each of the three sequential time frames, as well as their activation timecourses before and after learning. Initially, around 190 ms post-UP, a learning-related selective response to APW emerged in cortical areas surrounding the Sylvian fissure: aSTS, ventral premotor cortex, and the anterior part of intraparietal sulcus and insula. Once it appeared, differential activation in these areas was mostly sustained until response termination. After 250 ms, activation spread to more anterior brain regions, and by 330 ms post-UP it reached the pole of the left temporal lobe and the triangular part of the left IFG extending to its orbital part. Thus, the spatiotemporal pattern of semantic-learning-related neural activity in our study was generally consistent with the current hierarchical models of auditory word processing that imply the presence of an anterior-directed stream of word-recognition pathways (Hagoort, 2016; Hickok & Poeppel, 2016).

Table 2. Brain regions involved in “semantic” learning.

Cluster localization	**The most significant vertex within each cluster**				
	MNI coordinates (x, y, z)			T-value	p-value (uncorrected)
Ventral premotor (VPM) and opercular part of inferior frontal gyrus (IFG) **190 ms**	-52.64	20.44	17.64	-3.97	0.001
Insula and frontal operculum **265 ms**	-39.88	2.53	11.42	-3.76	0.001
Triangular and orbital IFG **325 ms**	-46.18	25.96	11.59	-3.33	0.003
Intraparietal sulcus (IPS) **190 ms**	-39.19	-43.38	37.83	-3.22	0.001
Anterior superior temporal sulcus (aSTS) **265 ms**	-46.45	-17.63	-12.15	-3.30	0.003
Temporal pole (TP) **325 ms**	-45.04	4.83	-25.58	-3.74	0.001

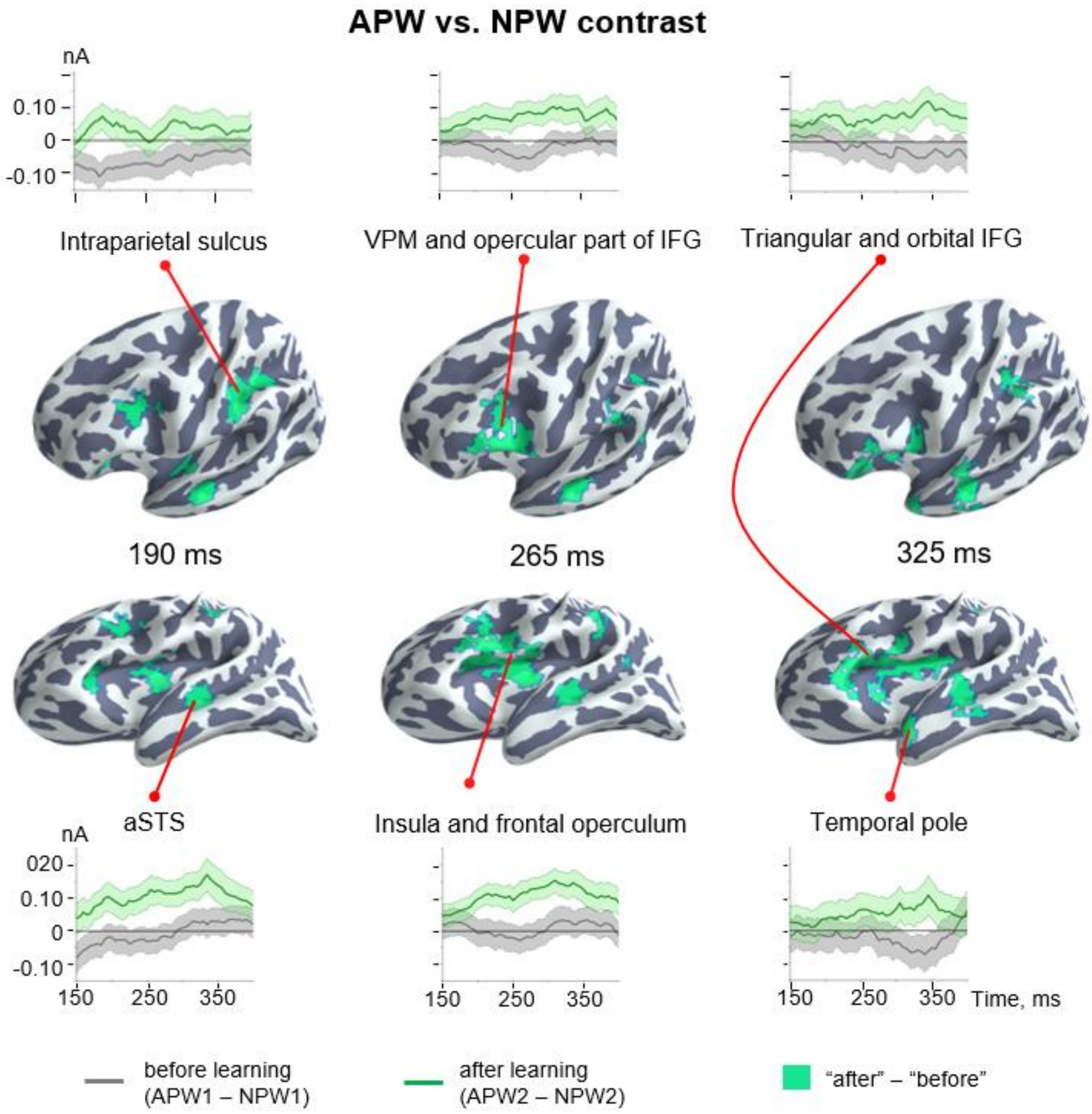

Figure 6. Spatial-temporal dynamics of the associative learning effect in source-space. Clusters of significant cortical vertices are derived for 35-ms time intervals centered on the peaks of the statistical significance obtained at the sensor-space (see text for details). Clusters are displayed on the cortical surface of the inflated left hemispheres shown at two different angles of view in order to better represent deep locations within the Sylvian fissure. The timecourses at the top and at the bottom represent grand-averaged differential response strength for the cortical clusters across time for "before learning" (APW1 - NPW1, gray lines) and "after learning" (APW2 - NPW2, green lines) conditions. Shaded areas on timecourses represent standard errors.

Discussion

Whether short-term learning of new words can induce rapid changes in cortical areas involved in distributed neural representation of the lexicon is a hotly debated topic in the literature. To answer this question, we examined the MEG phase-locked responses elicited in the cerebral cortex by passive presentation of eight novel pseudowords before and after an operant conditioning task. The task forced the participants to perform an active search for word-form meaning, as four unique word-forms acquired meaning that referred to movements of participants' own body parts (in a way similar to real action words) and the other four word-forms remained "empty lexical entities" associated with no particular meaning. By comparing learning effects between action-related (APW) and semantically "empty" (NPW) yet well-familiarized pseudowords, we expected to observe the emerging cortical signature of newly learned meaningful words.

There were three main findings in the current study. Deep familiarization with both APW and NPW acoustic word-forms led to a highly reliable and long-lasting suppression of cortical responses starting at around the UP in both hemispheres. Semantization of the new word-forms was followed by the learning-related increase in cortical activity to meaningful word-forms (APW) compared with meaningless ones (NPW) at around 150-400 ms after UP, which was lateralized to the left hemisphere. These learning-related changes in left-hemispheric cortical responses to semantically meaningful words were localized to the perisylvian cortex starting at approximately 150 ms, and to the higher-tier speech areas (temporal pole and triangular/orbital part of inferior frontal sulcus/gyrus) starting after 250 ms from the word-form UP. All of these learning effects were observed during passive presentations of the pseudowords that followed successful learning (greater than 90% accuracy) and repetitive performance of actions implied by the meaning of the newly learned words.

Our finding of a strong and highly reliable repetition suppression effect in the phase-locked response to repeated passive presentation of pseudowords in both categories stands in stark contrast to the previously reported EEG/MEG findings, according to which repetition suppression was characteristic for real words, while for pseudowords repetition caused the inverse effect, namely response enhancement (Kimppa et al., 2015; Shtyrov, 2011; Shtyrov et al., 2010). Notably, the repetition suppression effect in our data remained significant even we investigated exactly the same time interval, 50-150 ms after the word-form UP, which was previously reported to contain an enhanced evoked response to repeated pseudowords (*Figure 4*). How can stimulus repetitions have opposite effects on cortical responses depending on the way the stimuli were manipulated within the recent experience between the successive presentations?

Most probably, a degree of word-form familiarization, which might be collectively greater in the current experiment compared with the previous ones, is critically important for the sign of the neural repetition effect. The effect of repetition suppression is ubiquitous in the brain and well described for different sensory modalities (Gotts, Chow, & Martin, 2012; Grill-Spector, Henson, & Martin, 2006). Neural response reductions within a one-session stimulus repetition is thought to be indicative of formation of familiarization memory traces, which scales down the neural representation of the stimulus without sharpening it (McMahon & Olson, 2007; Weiner, Sayres, Vinberg, & Grill-Spector, 2010; for review, see Gotts et al., 2012). While “repetition-enhanced neural responses” were reported less frequently in the human literature, they are predominantly characteristic of the repetition dynamics for unfamiliar stimuli (Henson, Shallice, & Dolan, 2000) or for those with poor perceptibility (Turk-Browne, Yi, Leber, & Chun, 2007). Moreover, as demonstrated for a visual modality, repetition effects for unfamiliar stimuli can turn from enhancement to suppression when the number of stimulus repetitions increases, a phenomenon that possibly reflects a shift in neuronal responses depending on the degree of stimulus familiarity and on-line accessibility of its neuronal representation (Müller, Strumpf, Scholz, Baier, & Melloni, 2013). Since the cumulative number of repetitions for each pseudoword in our experiments (approximately 200) did not differ much from that used during passive presentations in the previous studies (160), the opposite sign of repetition effects could hardly result simply from a different number of stimulus repetitions. Yet, to continue this logic, another possibility is that deep familiarization with APW and NPW word-forms during our operant conditioning procedure completely changed the repetition effect: instead of increasing neural responses to previously unfamiliar word-forms, it decreased them when the word-forms became well-recognized concatenations of phonemes. Indeed, although we observed transient repetition-related changes in phase-locked ERF components elicited by auditory word onset well before the UP (*Figure 2*), a long-lasting and highly reliable attenuation of phase-locked activity occurred approximately 300 ms after stimulus onset, when the word-form began to be discriminable from each other. In fact, the onset of this reduction started even 100 ms earlier than UP, probably as a response to the appearance of the third phoneme in the word-form, which, unlike the UP, was not sufficient to distinguish all eight pseudowords, but rather allowed identification of the difference between APW-NPW pairs (see Methods for details).

The above considerations suggest that our findings of the strong suppression of neural responses to novel acoustic word-forms, which started to be very familiar through the experimental procedure, most probably reflect a mechanism of familiarization memory. This mechanism is one of the components of the recognition memory system that is responsible for judging the prior occurrence of a stimulus based on detecting stimulus familiarity. It is thought to be centered on the perirhinal structures of the medial temporal lobe that operates on neural representations in the neocortex, and it is associated with repetition suppression of neural responses to a familiar stimulus in perirhinal and neocortical structures that appear in one-session experiment and then last over days (Brown & Aggleton, 2001). Synaptic depression plasticity in the perirhinal cortex seems to play a critical role both in the activity-dependent suppression of neural responses and visual recognition memory (Griffiths et al., 2008). Repetition-sensitive neuronal phenomena (either suppressive or enhancive) accompany perceptual learning, and although they are unlikely to be its main underlying neural cause, they still might represent one of its mechanisms (Gotts et al., 2012; although for different opinions see McMahon & Olson, 2007).

While primarily determined by novelty/familiarity of a complex auditory stimulus, which is processed by the perirhinal cortex of the medial temporal lobe, repetition-sensitive neocortical responses are hardly indicative of learning-related neocortical plasticity. In other words, neither repetition suppression of phase-locked responses to novel word-forms found in our experimental settings nor the repetition enhancement effect resulting from their passive presentation (Kimppa et al., 2015; Shtyrov, 2011; Shtyrov et al., 2010) can be considered indicators of cortical "fast mapping" during word learning.

In order to conclude that experience-dependent modification of neocortical activity during word learning complies with the criteria of "fast mapping", one should at least provide evidence that (1) cortical electrophysiological responses to the unfamiliar word-forms are predictably and persistently modified by the experience obtained within a single experimental session, and index cortical plastic changes that lead to "experientially-induced tuning" toward a specific word-form neural representation, and (2) newly formed cortical representation is not only tuned to a particular concatenation of the phonemes but possesses referential meaning, i.e., its activation is linked to increased activation of the "semantic network" that encompasses multisensory higher-tier speech areas involved in semantic associations. The contrast between neural responses elicited by action-associated (APW) and non-associated (APW) pseudowords before and after operant conditioning answered the question to what extent the learning-related neural dynamic complies with these criteria.

Animal neurophysiological findings evidence that while neural activity in the auditory cortex decreases overall with stimulus repetition, firing rates become more selectively tuned toward stimuli that attain behavioral relevance, and the neural cells that encode such stimuli may maintain their firing rate levels or decrease them much less than other cells (Blake et al., 2006; Kato, Gillet, & Isaacson, 2015; Weinberger, 2004). If improved stimulus selectivity and sharpening of neural representations did occur for APW, we would expect that after operant conditioning, the cortical brain responses to APW would relatively increase compared with NPW. This finding is exactly what we observed while contrasting APW-NPW differences before and after learning (*Figure 6*).

Indeed, the only factor that affected the auditory perception of APW and NPW stimuli during the second passive presentation was their unique relatedness to a specific motor action in the prior active blocks. Acoustical features across APW-NPW pairs were well counter-balanced across the eight pseudowords (see Methods), and neural responses to pseudowords of both types did not differ before learning (*Figures 5 and 6*). Additionally, our findings cannot be explained by differences in selective attention to or in familiarization with APW-NPW pairs during learning. The learning procedure itself did not introduce any bias toward APW word-forms, as it required the subject to attentively discriminate between both stimulus types, which were repeated the same number of times and interleaved into pseudorandom sequences. Even with respect to action-relatedness, both types of pseudowords required a similar level of perceptual decision-making activity, because a subject had to either commit a motor response to the APW stimuli or refrain from it for NPW ones. Despite having behavioral relevance, NPW word-forms lacked unique referential meaning to a specific event, a core property of lexical items in human language. Thus, our results on experiential modification of human cortical responses to neutral auditory stimuli through an operant conditioning association procedure bears a striking resemblance to that described in single-cell recordings in monkey auditory cortex (Blake et al., 2006; Kato et al., 2015). These data may be considered as some of the first convincing evidence of rapid cortical plasticity in human neocortex.

Notably, unlike the early emergence of repetition suppression in the magnetic response timecourse to word-forms, the learning effect for APW-NPW contrast occurred relatively late in the phase-locked neural activity, starting not earlier then 140 ms after the word-form UP (*Figures 3 and 5*). At this point, the differential left-hemispheric response to APW encompassed mainly the anterior STS, ventral premotor cortex, insula/opercular part of IFG, and anterior IPS. These left perisylvian regions are heavily interconnected through the classic arcuate fasciculus pathway that connects superior temporal regions with extended Broca’s area, but also through a parallel pathway that projects the STS to the inferior parietal region. These routes are thought to participate in acoustic/phonological transcoding (Catani, Jones, & Ffytche, 2005). The recurrent motor-perceptual interaction is known to facilitate speech perception of unfamiliar speech stimuli, e.g., distorted speech and novel or low-frequency words (Stokes, Venezia, & Hickok, 2019; Wu, Chen, Wu, & Li, 2014). Therefore, greater involvement of the entire perisylvian network into the APW compared to the NPW response in our experiment may indicate that newly learned semantic association boosted perceptual processing of incoming novel linguistic stimuli.

Our interpretation is generally in line with the previous MMN results of Hawkins and colleagues, who described an increased MMN wave peak at 140 ms after the word UP in response to auditory pseudowords that acquired association with visual images (Hawkins, Astle, & Rastle, 2015). However, in our case, enhanced neural response to APW spanned 140 ms after the first meaningful phoneme and onwards, which clearly occurred later than the MMN wave. We speculate that rather than reflecting a rapidly detected phonological difference in the fourth phonemes between APW and NPW, the differential response to APW points to enhanced activity of neuronal circuitry that mediates sensitivity for the temporal sequence of the phonemes that corresponded to the coherent APW word-forms. There is ample evidence in the literature on the existence of higher-level auditory neurons that contain the combinatorial code for the whole auditory word-form and operate approximately 150-250 ms after the moment when a word-form becomes identifiable (Brink, Brown, & Hagoort, 2001; DeWitt & Rauschecker, 2012). In addition to later timing compared with the MMN, the APW differential response localization to the anterior superior temporal gyrus/superior temporal sulcus is compatible with its putative origin from higher-order combinatorial phonological representations of the entire word-form. Imaging studies localized processing of multisegmental word-forms to the left anterior STG/STS, downstream of the middle-posterior STS/STG, which underlies specific phoneme discrimination (Chang et al., 2010; DeWitt & Rauschecker, 2012). The strict left lateralization of our APW response (*Figure 4*) is also concordant with the putative site of auditory word-form recognition (see meta-analysis in DeWitt & Rauschecker, 2012).

Therefore, our findings suggest that the tuning of higher-order combination-sensitive neurons in aSTS for a word-form is contingent upon experience of its unique action relevance obtained within one experimental session. In other words, even short-term active search for auditory-action association, or effortful semantization of an "an empty word-like item" provided by our experimental settings, facilitates or even triggers strengthening of the cortical network that underlies the phonological aspect of lexicality: lexical representation of the respective coherent word-form.

The aSTS-centered cortical network, which is thought to contain lexical representations of real-word word-forms, does not store semantic information itself, but rather it interfaces with the semantic network that is widely distributed across the brain (DeWitt & Rauschecker, 2012). The question as to whether prolonged post-stimulus enhancement of neural responses to PW (*Figure 4*) reflects facilitated activation of features of the long-term memory representations that were briskly associated with a new lexical item. Our data may provide a tentative answer to this question. APW-related differential activation timecourses (*Figure 6*) suggest that after 200-250 ms, activation spreads from the perisylvian cortex toward more anterior cortical areas along both ventral and dorsal speech processing pathways (Rauschecker & Tian, 2000; Romanski, Tian, Fritz, Mishkin, & Rauschecker, 1999). Specifically, the activation timecourses in the ventral speech stream point to the later involvement of areas identified anatomically as the temporal pole, which was previously implicated in the semantic access (Binder & Desai, 2011; Ralph, Jefferies, Patterson, & Rogers, 2016). Concurrently, relatively delayed activation in the dorsal stream occurs in the triangular part of the IFG that encompasses the classical Broca's area as well as IFG orbital part, i.e., the left ventrolateral prefrontal cortex, thought to subserve controlled semantic retrieval (Ralph et al., 2016; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Localization of the late portion of the APW response to higher-order "semantic" cortical areas assumes that after learning, APWs selectively increase activity of the semantic network, i.e., attain the eminent property of the phase-locked cortical responses in the N400 range to real words compared with pseudowords (Cheng, Schafer, & Riddel, 2014).

Notably, the activity of the left-hemispheric aSTS and VPM speech areas involved in phonological processing of the auditory word-form persisted throughout the entire APW differential response from 150 ms until 360 ms after the word-form recognition point (*Figure 6*). This long-lasting activation of the phonological word-form representations is consistent with a principal of refining processing of complex stimulus features in hierarchical reentrant system (Bullier, 2001; Di Lollo, 2012) and may reflect recurrent interaction between different hierarchical levels of auditory word-form analysis. It is generally assumed that the main function of re-entrant signals is modulatory, and they may prolong and modify activity induced by bottom-up signals by way of integrating neuronal responses at each level of the pathway under the top-down influence from the higher order areas. From this view, we assume that while the early differential activity in the perisylvian areas appears to be stimulus-driven, the later activity there presumably depends on top-down signaling from higher-order speech cortical areas involved in semantic retrieval.

In summary, we would argue that according to criteria proposed by Davis & Gaskell (2009), and briefly reviewed here in the introduction, our data evidence that cortical representations of both phonology and semantics of previously unfamiliar words may be formed following 1-2 hours of active associative learning. This conclusion raises the question as to why a rapid cortical activity modulation by a newly learned word would be found in our MEG study, while the blood-oxygen-level-dependent (BOLD) response of cortical areas consistently remain largely unaffected during the hours after associative learning (Davis & Gaskell, 2009). There are two putative explanations for this discrepancy. First, the discordance between MEG/fMRI findings may result from different modes of neural activation captured by changes in an evoked, phase-locked response in the MEG and BOLD signals. Given that the BOLD signal integrates brain hemodynamic changes over several seconds, short-lived and synchronized neural activation that contributes to MEG/EEG phase-locked response could be difficult to detect with fMRI (Engell, Huettel, & McCarthy, 2012). Thus, a rapid formation of cortical representations of a newly acquired word may increase highly coherent cortical activation elicited by passive presentations of these stimuli; such coherent cortical activation is reflected in enhanced MEG phase-locked ERFs. A further strengthening of plastic cortical changes during a consolidation process might make them detectable using the fMRI recording technique.

Another explanation, which is not necessarily mutually exclusive with the first one, focuses on the difference in the associative learning procedure between our study and the previous fMRI research. The latter studies tested the involvement of cortical structures in adult experience-dependent neuroplasticity using paired-associative learning between auditory pseudowords and visual images. However, the findings of Blake and colleagues (Blake et al., 2006) demonstrated that the learning-induced increase in response selectivity of auditory neurons is observed following an operant conditioning, but not after passive reward-based associative learning. As the authors suggested, the successful reward-association plasticity that results from operant conditioning might be related to a greater involvement of neuromodulatory brain systems triggered by an increase in the subject’s motivation for active search for stimulus-action pairing. In other words, whether a new word will be learned depends on personal engagement into the learning process, wisdom that ages ago was recognized by psychological science: “Student engagement is the product of motivation and active learning. It is a product rather than a sum because it will not occur if either element is missing” (Barkley, 2009).

Materials and Methods

Participants

Twenty-four volunteers (mean age 24.9 years, range 19-33 years, 15 males) participated in the study. They were native Russian speakers with normal hearing and no record of neurological or psychiatric disorders. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). The study was conducted following the ethical principles regarding human experimentation (Helsinki Declaration) and approved by the Ethics Committee of the Moscow State University of Psychology and Education. All participants signed the informed consent before the experiment.

Stimuli and behavioral responses

The auditory stimuli (pseudowords) were created in such a way to precisely control and balance their acoustic and phonetic properties while manipulating their lexical status before and after learning. We used nine consonant-vowel (CV) syllables, which formed eight disyllabic ($C_1V_1C_2V_2$) novel meaningless word-forms (pseudowords). The pseudowords were built in compliance with Russian language phonetics and phonotactic constraints. After the associative learning procedure, four of them were assigned a unique action performed by one of four body extremities (action pseudowords - APW), while the other four implied no motor response (non-action pseudowords - NPW).

The first two phonemes (C_1V_1) formed the syllable ‘hi’ [xʲˈi] that was identical for all pseudowords used. The next two phonemes (C_2 and V_2) were independently counterbalanced across APW and NPW stimuli, and they were included in the two stimuli of each type, forming eight unique phonemic combinations (*Table 1*). This design ensured that acoustic and phonetic features were fully matched between the APW and NPW types (within respective pairs). The third phonemes (C_2), consonants *‘ch’* [t͡ɕ], *‘sh’* [ʂ], *‘s’* [s̪], *‘v’* [v], distinguished between the APW-NPW pairs by signaling which extremity a subject might be prepared to use (right hand, left hand, right foot, or left foot). All of the pseudo-words could only be recognized by their fourth phoneme (V_2: vowel *‘a’* [ə] or *‘u’* [ʊ]). The onset of the fourth phoneme will be referred to as “word-form uniqueness point” (UP; *Figure 1A*).

All stimuli were digital recordings (PCM, 32 bit, 22050 Hz, 1 channel, 352 kbps) of a female native Russian speaker’s voice recorded in a sound-attenuated booth. Four variants of three-phoneme combinations ($C_1V_1C_2$) and two variants of the last vowel (V_2) were recorded and then combined to generate eight pseudowords. All pseudowords were pronounced with stress on the vowel ‘i’ in order to match prosody between all the utilized pseudowords. The amplitude of the recorded stimuli was digitally equalized by maximal power, which corresponded to the stressed vowel ‘i’. For cross-splicing and normalization, sound recordings of the pseudowords were digitally processed using Adobe Audition CS6.5 software. The approximate duration of the spoken pseudowords was 530 ms. For all analyses, data were aligned on the word UP, which was kept at 410 ms after the onset of the audio recordings.

Additionally, two non-speech auditory stimuli were used as positive and negative feedback signals, each 400 ms in length. Both stimuli were complex frequency-modulated sounds that profoundly differed in their spectral frequency maxima (ranges were approximately 400-800 Hz for positive and 65-100 Hz for negative feedback), with spectral maxima increasing in frequency over time for the positive feedback and decreasing for the negative feedback.

Behavioral responses (*Table 1*) were recorded using hand-held buttons (package 932, CurrentDesigns, Philadelphia, PA, USA) pressed by the right or left thumb and custom-made pedals pushed by the toes of the right or left foot. For all of these movements, the actual trajectory was rather short (< 1 cm for buttons and < 3 cm for pedals), a design that minimized movement artifacts. Buttons and pedals interrupted a laser light beam delivered via fiber optic cable. Responses recorded from pedals and buttons were automatically labeled as ‘correct’ and ‘errors’ after each trial according to the task rules (see below).

Procedure

During the experiments, participants were comfortably seated in the MEG apparatus that was placed in an electromagnetically and acoustically shielded room (see below). Pseudowords were presented binaurally via plastic ear tubes in an interleaved quasi-random order, at 90 dB SPL. The experiment was implemented using the Presentation 14.4 software (Neurobehavioral systems, Inc., Albany, CA, USA).

The experiment consisted of four consecutive blocks with a fixed order across participants: (1) passive listening before learning, (2) active learning, (3) active performance, and (4) passive listening after learning (*Figure 1B*). The entire experiment lasted approximately 2 hours.

Two identical passive listening blocks were administered before and after the two active blocks. During auditory presentation, participants were offered to watch a silent movie projected on the screen positioned at eye-level 2 m away. Pseudowords were presented pseudo-randomly with an average interstimulus interval (ISI) of 1750 ms, randomly jittered between 1500 and 2000 ms at 1 ms steps (*Figure 1C*). Each passive listening block included 400 stimuli (50 repeated presentations of each of eight pseudowords) and lasted approximately 30 min.

After the first passive block, the participants were informed that during the following active blocks they had to find the association between each of the presented eight pseudowords and movements of their own body parts. To achieve this goal, they were asked to respond to each pseudoword either by using one of the four body extremities or committing no response, and then to listen to positive and negative feedback signals informing the participants whether the action was correct or erroneous. Instruction did not contain any other cues. The utilized behavioral procedure, which involved trying a variety of new auditory-action associations and eventually selecting only those that led to positive reinforcement, complied with the requirements of operant learning (Neuringer, 2002).

During the active learning block, participants were required to keep their gaze at the fixation cross in the center of the presentation screen in order to minimize artifacts caused by the participants' eye movements. The eight pseudowords were repeatedly presented within pseudo-random interleaved sequences. For each trial, a pseudoword was followed by a feedback signal, which was presented 2000 ms after the end of the pseudoword stimulus (*Figure 1C*). The average ISI (from the end of the feedback stimulus until the onset of the next pseudoword stimulus) was 2250 ms, randomly jittered between 2000 and 2500 ms at 1 ms steps. The feedback stimulus could be either positive or negative. Positive feedback was given if a participant complied with the task rues, i.e., committed a proper response to an APW stimulus or committed no response to an NPW stimulus (*Table 1*). The negative feedback followed three kinds of errors: (i) no response to an APW; (ii) a motor response to an APW performed with "the wrong extremity"; (iii) any response to an NPW. The number of stimuli in this block varied across participants depending on the individual success rate. An active learning block ended if a participant reached the learning criterion or if 480 stimuli were presented in total, whichever came first. Successful learning implied that a participant performed the correct responses in at least four out of five consecutive repeated presentations of each of the eight pseudowords. Whether a participant met the learning criterion was automatically checked after each trial. Out of 24 participants, two did not reach the learning criterion and thus went through all 480 trials in the learning block. Since their overall hit rate during the next active performance block was well within the range of performance of the other 22 participants, these two participants were not excluded from further analyses. The number of stimuli presented within the active learning block varied across participants from 74 to 480, with the respective inter-individual variation in the duration of active learning from 6 to 40 min.

Participants were then asked to repeat the same procedure (active performance block). The only difference between the two active blocks was that the active performance block included a fixed number of 320 trials and lasted approximately 30 min.

Short breaks were introduced between all blocks (10 min between the active performance block and the second passive block and 3 min between other blocks), during which participants were offered to rest while remaining seated in the MEG apparatus.

MEG data acquisition

MEG data were recorded inside a magnetically shielded room (AK3b, Vacuumschmelze GmbH, Hanau, Germany), using a dc-SQUID Neuromag VectorView system (Elekta-Neuromag, Helsinki, Finland) with 204 planar gradiometers and 102 magnetometers. For all recorded signals, the sampling rate was 1000 Hz, and the passband was 0.03-330 Hz. MEG was continuously recorded during each experimental block.

Participants’ head shapes were measured using a 3Space Isotrack II System (Fastrak Polhemus, Colchester, VA, USA) by digitizing three anatomical landmark points (nasion and left and right preauricular points) and additional randomly distributed points on the scalp. During MEG recording, the position and orientation of the head were continuously monitored by four Head Position Indicator coils.

The electrooculogram was registered with two pairs of electrodes located above and below the left eye and at the outer canthi of both eyes for the recording of vertical and horizontal eye movements, respectively. Bipolar electromyogram from the left dorsal surface of the neck over the trapezoid muscle was also recorded for the purpose of artifact detection.

After MEG data acquisition, participants underwent MRI scanning with a 1.5T Philips Intera system for further reconstruction of the cortical surface.

MEG preprocessing

Raw MEG data were first processed to remove biological artifacts and other environmental magnetic sources that originated outside the head using the temporal signal-space separation method (tSSS; Taulu, Simola, & Kajola, 2005) embedded in the MaxFilter program (Elekta Neuromag software). For sensor-space analysis, data were converted to a standard head position (x = 0 mm; y = 0 mm; z = 45 mm). Static bad channels were detected and excluded from further processing steps.

Artifact correction caused by the vertical and horizontal eye movements, eyeblinks and R-R heart artifacts was performed on continuous data in Brainstorm (http://neuroimage.usc.edu/brainstorm; Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) using the SSP algorithm (Tesche, Uusitalo, Ilmoniemi, Huotilainen, & Kajola, 1995; Uusitalo & Ilmoniemi, 1997).

Data from two passive blocks were divided into 1610 ms epochs (from -610 ms to 1000 ms relative to the UP). Epochs with increased muscle activity contribution were excluded by thresholding the mean absolute signal values within the high frequency range (60 Hz - 500 Hz) from each channel below 5 standard deviations of the across-channel average. After rejection of the artifact-contaminated epochs, the average number of epochs taken into analysis was 183 ± 21 and 182 ± 21 for APW and NPW stimuli, respectively, before learning, and 181 ± 21 and 182 ± 20 for the same stimuli after learning.

The baseline correction was computed using the interval from the -210 ms to 0 ms before the stimulus onset (i.e., -610 – -410 ms relative to the UP).

Data analysis

Analyses were performed in two steps. First, in search for the general familiarization effect for the novel word-forms, the phase-locked cortical responses to APW and NPW were compared between “before learning” and “after learning” conditions.

Secondly, we aimed to identify a putative effect of pseudoword associative learning on neural activity elicited by pseudowords that acquired referential meaning. To this end, we analyzed the APW-NPW difference in phase-locked responses before and after learning. We expected that while cortical responses to APW and NPW would not differ before learning, the differential response to APW would emerge after learning as a result of fine-tuning of cortical representations toward the respective auditory word-forms.

At each step, we analyzed MEG data both at the sensor- and the source-level in order to pinpoint the anticipated effects both in terms of their timing and involved cortical regions.

All further analyses were performed using MNE Python open-source software (http://www.nmr.mgh.harvard.edu/martinos) and custom-made scripts in Python.

Sensor-level analysis

For sensor-level analysis, we took MEG signal from planar gradiometers that are known to attenuate signals from distant cortical sources and in effect behave as spatial high-pass filters (Garcés, López-Sanz, Maestú, & Pereda, 2017; Vrba & Robinson, 2001).

Large groups of sensors depicted in *Figure 3* (*insert*) were chosen as ROIs for ERF analysis, separately for the left and the right hemispheres. Each of the two ROIs included 31 pairs of gradiometers that covered frontal, temporal, and parietal selections of MEG sensors. Such wide ROIs at the sensor level were used on the basis of a large body of literature that demonstrated speech processing effects are mostly observed in wide perisylvian areas, including temporal, insular, inferior frontal, and inferior parietal cortices (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Hagoort, 2016; Hickok & Poeppel, 2016).

The data were first combined within each gradiometer pair by calculating the root-mean-square values (RMS) and then averaged across channel pairs; such averaging was performed independently within each of the two ROIs under each of the four experimental conditions (APW1 and NPW1 before learning and APW2 and NPW2 after learning). The RMS signal was baseline-corrected using the interval from the -210 ms to 0 ms before the stimulus onset (-610 to -410 ms relative to the UP). A low-pass 6th-order Butterworth filter with a cutoff frequency 100 Hz was applied in order to smooth the RMS signals before statistical analyses; this procedure was done in order to reduce the signal-to-noise ratio.

Source-level analysis

Individual structural MRIs were used to construct single-layer boundary-element models of cortical gray matter with a watershed segmentation algorithm (FreeSurfer 4.3 software; Martinos Center for Biomedical Imaging, Charlestown, MA, USA)

The cortical sources of the magnetic-evoked responses were reconstructed using distributed source modeling. Source estimation was performed using unsigned cortical surface-constrained L2-norm-based minimum norm estimation implemented in the MNE software suite. A grid spacing of 5 mm was used for dipole placement, which yielded 10,242 vertices per hemisphere. The 'orientation constraint parameter,' which determines the extent to which dipoles may deviate from the orthogonal orientation in relation to the cortical surface, was set to 0.4. Depth weighting with the order of 0.8 and the limit of 10 was applied.

For source space analyses, the MEG recording was downsampled to 200 samples per second; each new sample was calculated as an average of five adjacent timepoints for each channel independently. Time window before stimulus onset (from -610 to -410 ms) was used as a baseline.

Familiarization effects (sensor-level analysis)

In order to reveal the time interval during which the familiarization effect was significant for both types of pseudowords, we collapsed the data across APW and NPW trials. Then, the RMS signals were separately contrasted for “after learning” versus “before learning” conditions for each hemispheric ROI. A paired two-tailed t-test was applied at each time point of the data within -410 to 1000 ms relative to the UP. In order to enhance statistical power and provide correction for multiple comparisons, we applied the TFCE method; this approach takes into account both data point statistical intensity and its neighborhood via computing a "supporting area" for each data point (Mensen & Khatami, 2013). The permutation procedure involved 1,000 repetitions on surrogate data, which were generated from real data by swapping the two conditions for the entire time window in random subsets of participants. The significance level was set at $p < 0.05$ (corrected). Then, we repeated the same analysis separately for action pseudowords (APW2 versus APW1) and non-action pseudowords (NPW2 versus NPW1).

For illustrative purposes, the differential (after learning minus before learning) topographic maps for ERFs elicited by APW and NPW stimuli separately were plotted in 100 ms steps (data averaged across 35 ms for each plot).

Additionally, although not the main purpose of the current study, we analyzed early transient familiarization effects bound to the stimulus onset that, although prominent, did not survive the TFCE correction procedure. For this purpose, all trials were pooled, we averaged over timepoints within the 35-ms intervals centered on M100 and M200 peaks, and applied a paired two-tailed t-test (for each hemisphere separately).

Familiarization effects (source-level analysis)

Cortical sources that exhibited the familiarization effect were reconstructed for time windows during which the effect was significant at the sensor level in the left and right ROIs (see above). The source-space data for APW and NPW types were collapsed and averaged over these time intervals. We compared “before learning” and “after learning” conditions using vertex-wise t-test with FDR correction performed for two hemispheres (20,484 vertices).

Next, for the sake of comparison with the previous passive word learning studies, two successive intervals were chosen within the obtained time window. The earlier interval (50-150 ms after UP) exactly matched the one previously reported to demonstrate the ultra-rapid effects of word learning and discrimination (Kimppa et al., 2015; Macgregor et al., 2012; Shtyrov, 2011; Shtyrov et al., 2010). The later interval (150–400 ms) covered the timing of the significant semantic learning effect (see below).

Within each time window, the source-space data for APW and NPW types were pooled together and averaged over time intervals of interest (50-150 and 150-400 ms after UP). After splitting the two time windows should be considered as exploratory, so the “before” and “after” learning conditions were compared using vertex-wise t-test with FDR correction performed for two hemispheres (20,484 vertices).

Semantic learning effects (sensor-level analysis)

We sought to identify the semantic learning effect by analyzing the contrast between cortical responses to APW and NPW types before and after learning.

First, the statistical analyses were performed for the contrast "APW1-NPW1" versus "APW2-NPW2", where APW1 and APW2 stand for ERF time course to passive presentation of APWs "before learning" and "after learning", respectively, while NPW1 and NPW2 designate the responses to NPWs under the same two experimental conditions. The paired t-test with the TFCE permutation statistical procedure (see above for details) was applied at each time point of the entire RMS waveform (from -410 ms to 1000 ms relative to UP) to determine the response intervals that demonstrated a significant difference between conditions. To ensure that the APW-NPW difference in the neural responses before and after learning did result from learning, we additionally checked for the significance of the APW-NPW difference for each of the two conditions separately ("before learning" and "after learning") using the same TFCE permutation statistical procedure.

To visualize the direction and dynamics of the effect, we plotted ERF topographic maps for the (APW – NPW) difference before and after learning at 100 ms steps; at each step we integrated the ERF signed values across 35 ms.

Semantic learning effects (source-level analysis)

To reveal cortical regions, activation of which contributed to the "semantic learning" effect, the cortical sources of the effect were reconstructed within the time interval that was identified at the sensor level. Since for the sensor-level data the effect already survived correction for multiple comparisons, for source-space analysis we applied the uncorrected significance threshold of $p < 0.05$ (see Gross et al., 2013). To this end, we used a vertex-wise paired two-tailed t-test in order to contrast cortical activity averaged across the whole time interval for APW1 versus NPW1 ("before learning") and for APW2 versus NPW2 ("after learning"). Further, in order to explore the temporal dynamics of the semantic learning effect, we used a vertex-wise paired two-tailed t-test in order to contrast cortical activity for "APW1-NPW1" versus "APW2-NPW2" differences between conditions. This was done at the time points corresponding to the lowest p-values ($p < 0.01$) of the effect within the time interval that was identified at the sensor level. We averaged the source strength over 35-ms time intervals centered on the respective time points and considered only large cortical clusters including more than 20 adjacent vertices that demonstrated above-threshold significant effect at the respective time points. We then reconstructed activation timecourses for the obtained clusters.

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Competing interests

Authors have no financial and non-financial competing interests.

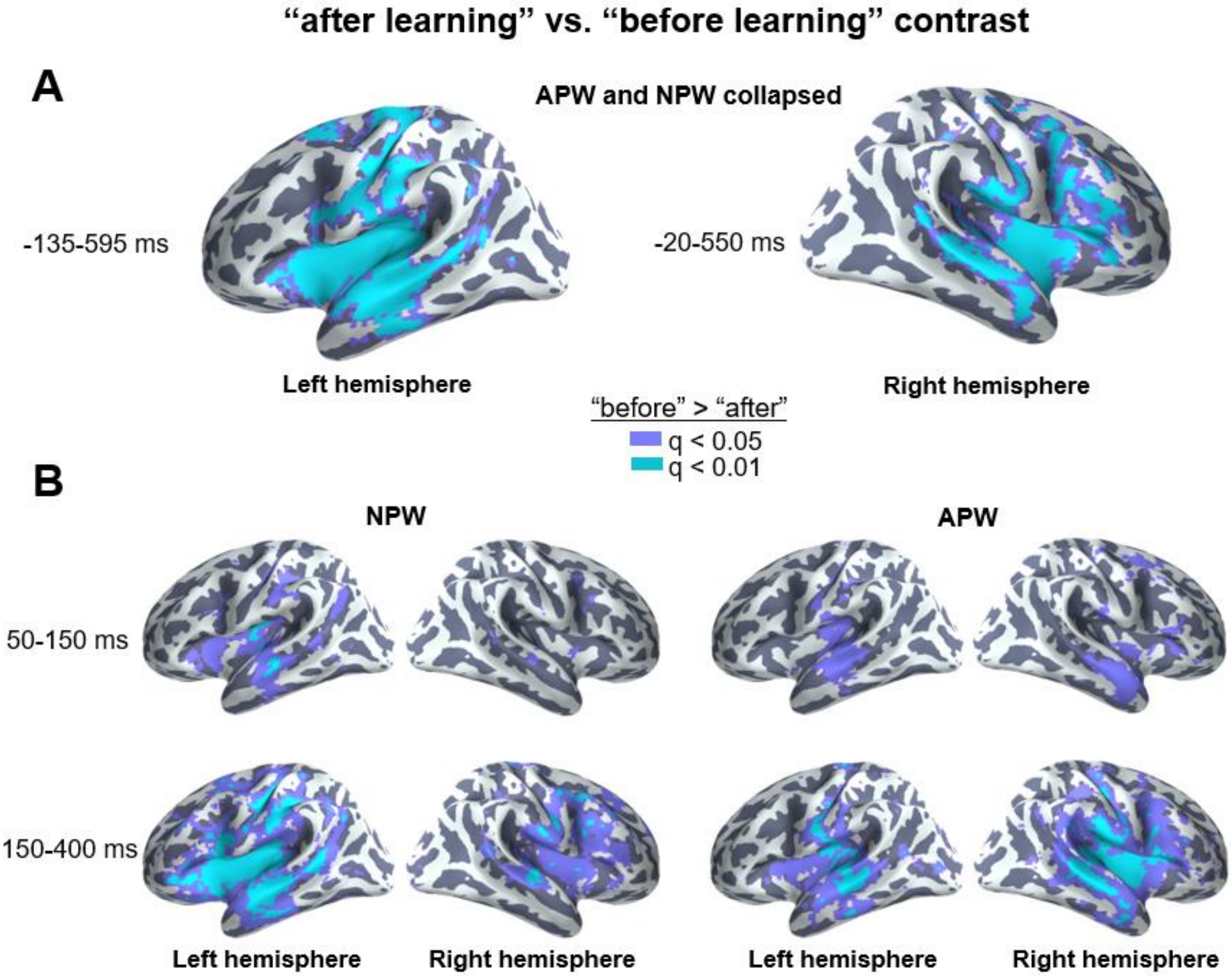

Figure 3 - Supplementary Figure. The repetition suppression effect in the source-space. Statistically thresholded maps (voxel-wise paired T-test, FDR-corrected, q < 0.05 and q < 0.01 are shown in purple and light-blue colors, respectively) for “after learning” versus “before learning” contrasts. **(A)** Analysis performed on the data averaged across the whole-time interval detected by the RMS analysis, with the APW and the NPW conditions collapsed. **(B)** APW and NPW stimuli analyzed separately. Results are represented for two time windows: early (50-150 ms after the UP) and late (150-400 ms).

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