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Physiology of Higher Nervous (Cognitive) Activity in Humans

# Prolongation of Cerebral Activation in Response to a Stimulus as a Probable Mechanism of Associative Plasticity during Semantic Learning

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Remembering the meanings of new spoken words is believed to occur as a result of associative learning. For example, this is how words denoting movements can be compared with their corresponding motor acts. Synaptic plasticity is known to develop in the brain when the activity of the cellular ensembles representing associated events coincides in time. However, in reality, such associations can develop when there is a significant time gap between the events to be associated, violating the conditions required for the occurrence of synaptic plasticity. We suggested that the conditions required for the development of synaptic plasticity in the brain can be created if the activity of neural representations is prolonged in time such that the required overlap in time at the level of neural ensembles is achieved. To test this assumption, we recorded magnetoencephalograms from voluntary participants during the development of associations between pseudowords and movements of the four limbs. The results obtained here show that there is indeed a significant prolongation of stimulus-induced auditory-verbal activation when new associations develop. Thus, during the development of an association, conditions can be created in the brain for the development of Hebbian plasticity, even if the associated events are separated in time.

**Keywords:** associative learning, reinforcement learning, memory, words associated with actions, evoked fields, magnetoencephalography.

**Introduction.** The current view of how new speech words are memorized is based on the neurobiological mechanisms of associative learning [Barsalou, 2003; Pulvermuller, 2005, 2018], i.e., processes of synaptic plasticity connecting two representations develop when the meanings of words are learned. For example, in the case of learning the meanings of words denoting movements, this could consist of associating the sound of a word with the execution of a physical movement. If the corresponding populations of neurons in the auditory and motor areas are activated simultaneously, this can lead to strengthening of synaptic connections and the formation of distributed cellular ensembles [Hebb, 1949]. Once such plastic rearrangements have developed, isolated presentation of an auditory stimulus begins to activate both neuron populations.

Indirect evidence that the Hebbian learning principle is applicable to human speech was provided by neuroimaging results on associative reactivation in the auditory and somatotopically organized motor areas of the cerebral cortex, induced by auditory presentation of words denoting actions (see, for example, [Shtyrov et al., 2014]). In addition, implementation of this principle was confirmed by computational modeling of the acquisition of action words [Tomasello et al., 2017]. However, these studies used real words of the language well known to the experimental par-

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ticipants, while there are very few studies in the literature of associative plasticity formed directly during experiments addressing the establishment of new associations between auditory pseudowords and specific actions (for review see [Razorenov et al., 2020]).

Furthermore, to our knowledge, none of these studies examined changes in neural activity when the associated events were temporally separated (e.g., [Naya et al., 2003]). Research of this type could, however, clarify unresolved questions regarding the putative mechanisms of associative word learning which rely on temporal correlations between auditory presentation of words and motor actions.

The weak point of current concepts of the associative nature of the mechanism establishing correspondences between words and actions is precisely the assumption that auditory activation induced by the corresponding action-denoting word and motor commands in the motor cortex occur almost simultaneously (see, for example, [Pulvermuller, 2018]). However, in natural environments, during such learning, the word and the action associated with it may not coincide in time – with discrepancies of up to several seconds or more – which is definitively more than what is permissible for the formation of Hebbian plasticity. Thus, explanation of the learning of action-denoting words through associative synaptic plasticity requires an understanding of the neurophysiological mechanisms allowing synaptic plasticity to evolve despite such significant temporal separation of the events to be associated.

One approach to solving this problem is based on the suggestion that the process of developing an association between a word and an action involves new words coming to evoke longer auditory responses, allowing them to overlap in time with the moment of initiation of the corresponding motor command. Since Hebb formulated his principle more than 50 years ago [Hebb, 1949], there has been a hypothesis that activity is maintained by synaptic reverberation in recurrent chains of connections between neurons [Shu et al., 2003].

This possibility was confirmed by single-neuron recordings in monkeys, which demonstrated sustained excitation in neurons in the temporal cortex during a task consisting of retaining a visual image in short-term memory [Miyashita and Chang, 1988]. This process may involve descending pathways from the frontal cortex initiating retrospective retention of a sensory representation relevant to the current task. The role of the prefrontal cortex in anticipating events and integrating them over time is well described in studies on monkeys [Funahashi et al., 1989; Fuster and Bressler, 2015; Quintana and Fuster, 1999]. This leads to the expectation that activity in the auditory cortex in the human brain will increase during the formation of an auditory-motor association simultaneously with the development of the rule linking the auditory stimuli presented with the corresponding motor responses.

This retrospective activation hypothesis predicts that the duration of the neural response evoked by presentation of a new word for which an association with a particular action is to be formed should increase as the association is formed. It can therefore be suggested that auditory-verbal activation in the temporal areas will be increased and prolonged during the process of learning.

The present study used magnetoencephalography (MEG) to determine whether the active formation of associations between pseudowords and actions leads to corresponding changes in cerebral activity following presentation of an auditory stimulus.

Our recent research using MEG in adults addressed the rapid formation of associations between pseudowords and actions which occurs directly during experiments [Razorenova et al., 2020]. We showed that passive listening to pseudowords previously associated with particular motor actions induces specific differential activation of the brain in the auditory and other language areas of the left hemisphere, as compared with similar pseudowords presented the same number of times but without developing an association with actions [Razorenova et al., 2020]. The occurrence of such differences in neural responses provides evidence that learning by active association leads to the development of rapid cortical plasticity in the adult auditory cortex; this result was a necessary prerequisite for the present study.

The present work seeks to carry out a direct examination of the learning process which may enable the plasticity observed in our studies; here we therefore analyzed the active learning and execution phases in the same experiment [Razorenova et al., 2020]. Experimental participants were presented with a set of eight pseudowords, associated and not associated with the action during the experiment; the association of these pseudowords with the movement of various parts of the body or inaction was gradually established by the participants through learning by trial and error. Cerebral activity at the early and advanced stages of associative learning was compared. The expectation was that there would be an increase in and prolongation of auditory stimulus-evoked activation at the advanced stage of learning as compared with the early stage.

**Methods.** ***Experimental participants.*** A total of 29 right-handed, native Russian-speaking subjects voluntarily took part in the study (mean age 24.7 years, range 19–33 years, 18 men). All participants had normal hearing and did not suffer from neurological or psychiatric disorders. The study was conducted in compliance with the ethical principles of human experimentation (Declaration of Helsinki) and was approved by the Ethics Committee of the Moscow State University of Psychology and Education. All participants signed informed consent before starting the experiment.

***Stimuli and experimental procedure.*** Auditory stimuli (pseudowords) were designed such that their acoustic and phonetic properties were counterbalanced (see [Razorenova et al., 2020] for a detailed description). Syllables composed of one consonant and one vowel (CV) were used to construct eight two-syllable ($C_1V_1C_2V_2$) nonsense pseudowords.

TABLE 1. Correspondence between Stimuli and Behavioral Responses in an Experimental Association Task

| Pseudoword associated with movement (MP) | | Pseudoword not associated with movement (NMP) | |
|---|---|---|---|
| pseudoword | movement | pseudoword | movement |
| *khicha* | Left hand | *khichu* | No movement |
| *khishu* | Left foot | *khisha* | No movement |
| *khisa* | Right foot | *khisu* | No movement |
| *khivu* | Right hand | *khiva* | No movement |

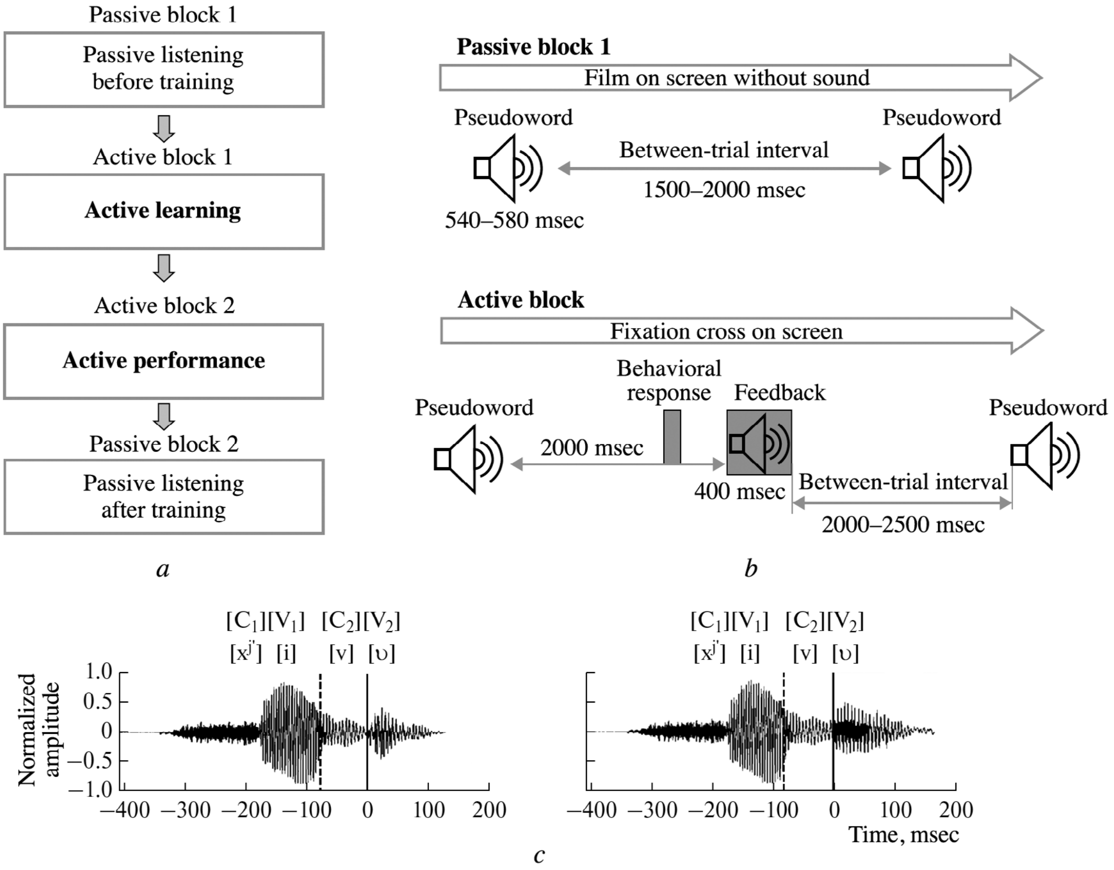

Fig. 1. Experimental procedure. *a*) Sequence of experimental blocks. *b*) Temporal structure of passive and active experimental blocks. *c*) Examples of pseudowords used as stimuli in the experiment (“khivu” and “khiva,” at left and right, respectively). The zero value on the time scale and the vertical solid line indicate the beginning of the fourth phoneme the (pseudoword disambiguation point); the vertical dotted line marks the beginning of the third phoneme.

During the associative learning procedure, four of these stimulus words were associated with a unique action performed by one of the four limbs of the body (movement-associated pseudowords (MP), i.e., “words” that acquired meaning), and the remaining four indicated the absence of a motor response (non-movement-associated pseudowords, NMP).

In the pseudowords created for the present experiment, the first two phonemes ($C_1V_1$) formed the syllable “khi” [x$^{j'}$i], which was identical for all the pseudowords used. The next two phonemes ($C_2$ and $V_2$) were balanced between the MP and NMP stimuli in such a way as to ensure a complete match of acoustic and phonetic characteristics between the two types of stimuli (Table 1). The third phoneme ($C_2$), the consonants “ch” [t͡ɕ] “sh” [ʂ], “s” [s̪], and “v” [v], occurred in both MP and NMP stimuli and signaled which limb the subject should use (right arm, left arm, right leg, or left leg). The fourth phoneme ($V_2$: vowel “a” [ə] or “u” [ʊ]) was counterbalanced between the MP and NMP conditions. Thus, only the fourth phoneme allowed unambiguous recognition of all pseudowords. Its beginning will henceforth be called the “disambiguation point” (Fig. 1, *c*).

As can be seen from Table 1, the phonetic composition of the stimuli and the stimulus-response mapping corresponded to a full within-subject counterbalanced design for the third and fourth phonemes, as well as for left/right and upper/lower limb movements.

All stimuli were digitally recorded in a female voice by a native Russian speaker in a soundproof booth. All pseudowords were pronounced with emphasis on the first vowel "i". The amplitude of the sound recordings was equalized to maximum power. Cross-splicing and normalization of the recorded stimuli were carried out using the Adobe Audition CS6.5 program. The average pseudoword duration was approximately 530 msec.

Two non-speech sounds, each lasting about 400 msec, were used as positive and negative feedback signals. Motor responses performed by the hands were recorded using buttons (package 932, CurrentDesigns, USA), which the experimental participants pressed with the thumb of their right or left hand, and leg movements were recorded using pedals pressed by the toes of the right or left foot (Table 1). Responses recorded from the pedals and buttons were automatically marked as "correct" or "incorrect" after each trial in accordance with the rules of the task (see below).

Throughout the experiment, participants sat comfortably in a chair in a MEG machine in a shielded room (see below). Pseudowords were presented binaurally through plastic ear tubes in an alternating quasi-random order at a volume level of 60 dB SPL. The experiment was conducted using Presentation 14.4 software (Neurobehavioral systems, Inc., Albany, CA, USA).

The experiment consisted of four blocks: (1) passive listening before training, (2) active training, (3) active performance, and (4) passive listening after training (Fig. 1, *a*). The entire experiment lasted about 2 hours. The present study analyzed data for two active blocks (results for passive blocks have been presented previously [Razorenova et al., 2020].

After completing the first passive block, participants were instructed that during the next active blocks they were to make an unambiguous association between each of the eight pseudowords presented and the movements of their own arms and legs. To do this, they must either respond to each pseudoword using one of the four limbs of the body or refrain from mounting a motor response. They then listened to positive and negative feedback signals that told them whether the action was correct or incorrect. This behavioral procedure involved participants trying different movements and ultimately selecting those which resulted in positive reinforcement, consistent with operant learning [Neuringer, 2002].

In the active blocks, participants were asked to hold their gaze on a fixation cross in the center of the screen to prevent eye movement artifacts. The eight pseudowords were presented in pseudorandom order. The feedback signal was supplied in all trials in the active blocks. Positive feedback was given if the participant complied with the rules of the task, i.e., made the correct movement in response to the MP stimulus and did not make any movement in response to the NMP stimulus (Table 1). Negative feedback followed three types of errors: (1) failure to respond to MP, (2) motor responses to MP performed by the "wrong limb," (3) any response to NMP.

Feedback signals were presented 2000 msec after the end of the pseudoword (Fig. 1, *b*). The interval between trials (from the end of the feedback stimulus to the beginning of the next pseudoword) varied randomly from 2000 to 2500 msec.

The number of stimuli in the active learning block depended on each participant's learning rate: the block ended if the participant reached the learning criterion or if a total of 480 stimuli were presented, whichever came first. The learning criterion required the participant to respond correctly to at least four of five consecutive presentations of each of the eight pseudowords. Two participants did not reach the learning criterion and thus progressed through all 480 trials in the learning block. Given that the overall proportions of correct responses during the next block of active performance for these participants were within the same range as for the others, we did not exclude them from further analysis.

In the next active performance block, participants were asked to repeat the same procedure. The only difference between the two active blocks was that the active execution block included a fixed number of 320 trials and lasted approximately 30 min.

Participants were offered short breaks between blocks.

***Recording of magnetoencephalographic data.*** Experiments were carried out in an electromagnetically and acoustically shielded room (AK3b, Vacuumschmelze GmbH, Germany). MEG traces were recorded using the dcSQUID Neuromag VectorView system (ElektaNeuromag, Finland), which has 306 MEG channels (204 planar gradiometers and 102 magnetometers). MEG signals were recorded with a 0.1–330 Hz bandpass filter, digitized at 1000 Hz, and stored for subsequent analysis.

Participants' head shapes were measured using the 3Space Isotrack II System (Fastrak Polhemus, Colchester, USA) by digitizing three anatomical reference points (nasion, left and right preauricular points) and an additional randomly distributed 60–100 points on the scalp. Head position and orientation were continuously monitored during MEG recordings using four HPI coils.

Biological artifacts and other sources of magnetic fields originating outside the head were removed from the MEG data using the Temporal Signal–Space Separation Method (tSSS) [Taulu et al., 2005] implemented in MaxFilter (standard Elekta Neuromag software). For further analysis at the sensor level, MEG data were converted to a standard head position ($x = 0$ mm; $y = 0$ mm; $z = 45$ mm).

Biological artifacts (caused by eye movements, blinks, and heartbeats) were corrected on continuous data in the Brainstorm program [Tadel et al., 2011] using the SSP algorithm [Uusitalo and Ilmoniemi, 1997].

Epochs (from –500 to 1500 msec relative to pseudoword onset, see below) with muscle artifacts were excluded from the analysis by calculating the mean absolute values of the signal filtered above 60 Hz on each channel. Epochs in which maximum amplitudes in more than a quarter of the

TABLE 2. Behavioral Indicators of Task Performance

| Behavioral indicators | Active learning (active block 1)[1] | Active performance (active block 2)[1] | Active learning versus active performance, Student's t test | |
|---|---|---|---|---|
| | | | T(28) | *p* |
| Correct responses to pseudowords associated with movement, % | 68 ± 9.6 | 95.6 ± 5.4 | –13.2 | <0.0001 |
| Correct responses (i.e., absence of movement) to pseudowords not associated with movement, % | 68.1 ± 7.1 | 97.2 ± 4.1 | –20.2 | <0.0001 |
| Total correct responses, % | 68 ± 6.2 | 96.4 ± 4 | –22.2 | <0.0001 |
| Errors: incorrect movement in response to pseudowords associated with movement, % | 16.1 ± 5.9 | 1 ± 1.4 | 12.5 | <0.0001 |
| Errors: absence of movement in response to pseudowords associated with movement, % | 15.9 ± 7.1 | 3.4 ± 5.1 | 8.0 | <0.0001 |
| Errors: false alarms in response to pseudowords not associated with movement, % | 31.9 ± 7.1 | 2.8 ± 4.1 | 20.2 | <0.0001 |
| Reaction time, msec | 1492.5 ± 101.1 | 1352.9 ± 116.3 | 8.4 | <0.0001 |

[1] Mean ± standard deviation.

channels exceeded five standard deviations from the mean across all channels were excluded from the analysis.

***Behavioral indicators.*** Participants' performance on the task was assessed in terms of (1) the mean number of correct responses to the four pseudowords associated with movements (MP) and the four pseudowords not associated with movements (NMP; where the correct response was no movement), and (2) the mean reaction time on performance of motor responses to pseudowords(MP); both indicators were assessed separately in two active blocks, i.e., at the early and late active learning stages (ELS and LLS conditions, respectively) (Table 2). Learning curves were constructed by calculating the accumulated numbers of correct responses within each block as a function of the number of trials in that block (see, for example, [Gallistel et al., 2004]). The slope of the curve shows the current level of task completion. To visualize the overall progress of learning and the asymptotic level of performance at the group level, the proportions of subjects who gave correct responses in the ELS and LLS conditions, respectively were also plotted (Fig. 2).

***Selection of epochs for analysis.*** Our objective was to test whether late auditory activity can be increased and prolonged during active learning, so our interest was in comparing the early and advanced stages of associative learning (ELS and LLS, respectively). We extracted the earliest trials from active block 1 ("early stage of learning" condition, ELS) and the latest trials from active block 2 ("advanced stage of learning" condition, LLS), and did this separately for the two types of trials – with motor response (MP) and without motor response (NMP). For each condition, we aimed to extract up to 80 trials if the number of artifact-free trials was sufficient to do so. If fewer than 40 trials were collected in at least one of the conditions, then the corresponding participants were completely excluded from further analysis; thus, MEG data were analyzed in a cohort of 24 participants.

We then identified epochs from –500 to 1500 msec relative to the onset of the pseudoword. The baseline was adjusted using a pre-stimulus interval from –500 to –50 msec before the onset of stimulus presentation.

***Sensor-level analysis.*** To reduce the size of the dataset and the volume of multiple comparisons, we calculated the root mean square values of evoked fields (EF) separately for each pair of gradiometers (henceforth termed combined gradiometers). After this transformation, analysis was run at the sensor level on 102 channels. Root mean square values of the EF between all gradiometers were calculated to analyze and illustrate the dynamics of EF over time, which yielded global rms EF values (analogous to global field power in the EEG).

Root mean square values of VP were calculated using the following equation:

$$\begin{aligned} RMS = \{[(ch\_1^2_{planar1} + ch\_1^2_{planar2}) + \ldots + \\ + (ch\_n^2_{planar1} + ch\_n^2_{planar2})]/N_{ch}\}^{1/2}, \end{aligned} \tag{1}$$

where $N_{ch}$ is the number of planar gradiometers $ch\_n_{planar1}$ and $ch\_n_{planar2}$ are the values of the planar gradiometers in orientations 1 and 2, and $n$ is the index of the gradiometer pair.

Root mean square values were calculated sequentially at each time point and the resulting time dynamics were presented on the corresponding graphs. Global root mean square EF (i.e., averaging over all gradiometers) were constructed for all conditions in active blocks together, for each condition in active blocks separately, and also additionally for the first passive block. The significance of differences between conditions was assessed using a two-tailed paired *t* test with the FDR correction for multiple comparisons for the number of time points.

The hypothesis that stimulus-related activity increases and is prolonged during the advanced stage of learning was tested by seeking differences between the ELS and LLS conditions. We expected learning-induced changes to lead to an

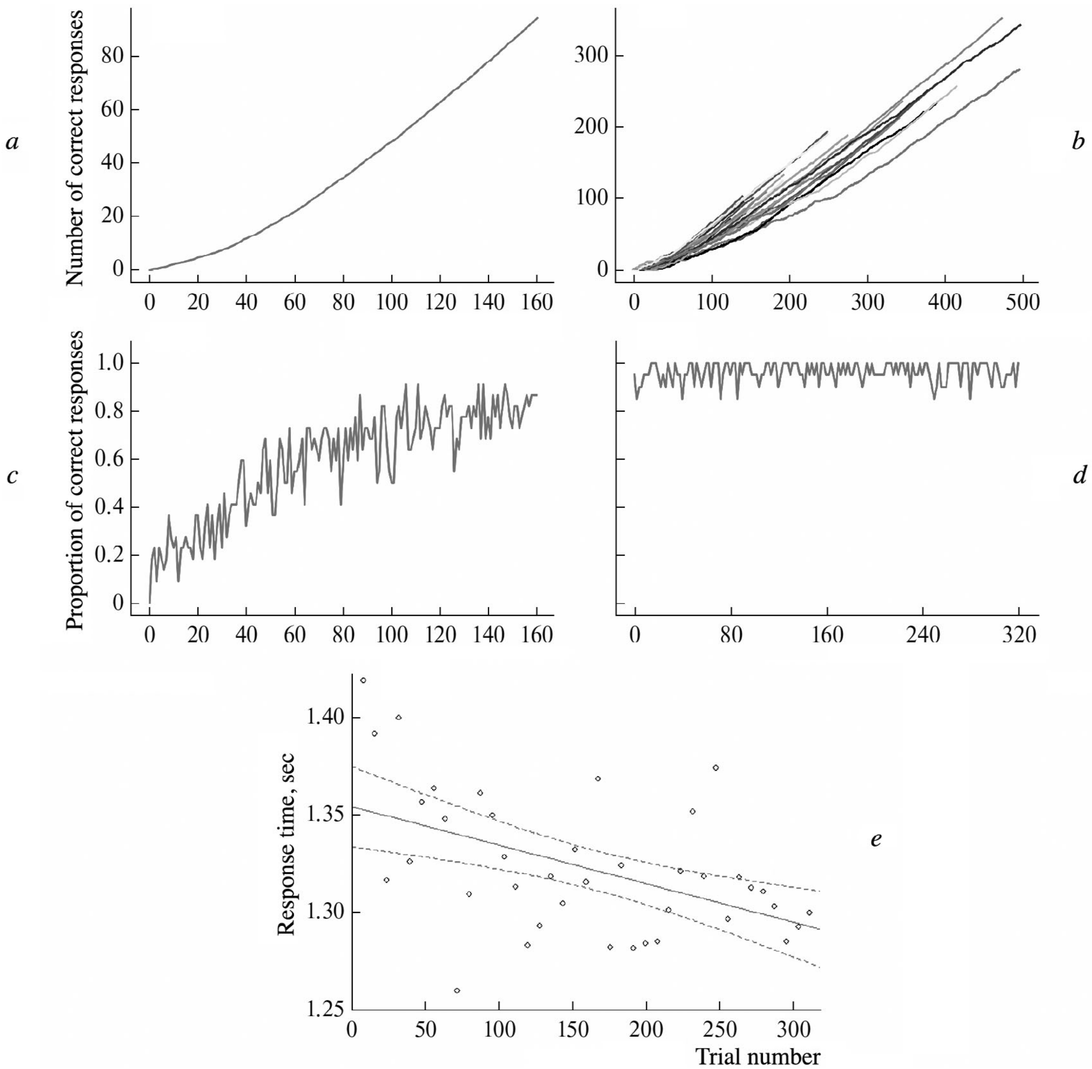

Fig. 2. Development of associations between pseudowords and movements during active learning. Top panels: cumulative level of performance on the associative task in active block 1, overall mean (*a*) and individual data for each experimental participant (*b*). Here and below, trial numbers are plotted on the horizontal axis (40 trials from the beginning of active block 1 for each limb, and the entire active block 2). Middle panels: Proportions of correct responses in the group of subjects depending on trial number in active block 1 (*c*) and in active block 2 (*d*). Bottom panel (*e*): Scatterplot of reaction time as a function of trial number in active block 2 (each point represents the mean of the reaction times over four consecutive trials). Solid and dotted lines represent the linear regression ($R^2 = -0.26$; $p < 0.001$) and the 95% confidence interval, respectively.

increase in the duration of stimulus-evoked neural activation for both MP and NMP trials, but that the greatest prolongation of the differential neural response would be seen for newly learned action-associated pseudowords (MP).

To avoid bias, time intervals and sensors of interest were selected for subsequent analyses without making any a priori assumptions, i.e., selection was guided directly by the data (taking into account the required corrections for multiple comparisons) and the following steps were run. First, the time of the maximum EF in response to pseudowords regardless of condition was determined: this was done by averaging the root mean square values of EF between all combined gradiometers across all four active block conditions, sequentially at each time point. Further analysis used a 100-msec time interval centered on the identified response peak and this was used to analyze all conditions in the active blocks.

Those combined gradiometers whose signals, averaged over the time interval of the maximum response described above, were significantly influenced by learning were then sought. Statistical comparisons between ELS and LLS were then run in all 102 channels, separately in MP and NMP trials. Sensors in which the significance level was below 0.05 (taking into account the FDR correction for 102 combined gradiometers) were taken as significant. Spatial clusters of significant sensors were defined as sets of reliable sensors located on a topographic map in close proximity to each other, and simultaneously significant for both MP and NMP trials. This analysis allowed two clusters of combined gradiometers to be identified – left temporal and median (see Results).

Further spatiotemporal analysis for each cluster was by averaging the root-mean-square EF values across all three combined gradiometers within each cluster. Graphs of the resulting root-mean-square EF values were then plotted and their values in the LLS and ELS conditions were compared between trials that included motor responses to presentation of pseudowords (MP) and trials not accompanied by limb actions (NMP).

To visualize the time dynamics at the sensor level, topographic maps were constructed for 102 combined gradiometers in the MP and NMP trials, for the early and advanced stages of training, along with topographic maps of the differential response to learning for each type of trial (LLS MP vs. ELS MP; LLS NMP vs. ELS NMP).

Repeated measures ANOVA was used for statistical analysis of the expected differential prolongation of the cerebral response to learned MP pseudowords compared to NMP pseudowords. For this purpose, the time interval corresponding to the gradual decline of the global root mean square EF was divided into four consecutive segments (850–1000, 1000–1150, 1150–1300, and 1300–1450 msec after stimulus onset). The root mean square values of the EF averaged over each time segment for each of the clusters served as the dependent variable. The analysis factors were Stage of learning (ELS and LLS), Type of trial (MP and NMP), Topography (left temporal and medial clusters), and Time (850–1000, 1000–1150, 1150–1300, and 1300–1450 msec after stimulus onset). The number of degrees of freedom was adjusted using the Greenhouse–Geisser correction. Planned post hoc comparisons were used to assess differences between MP responses (LLS minus ELS) and NMP responses (LLS minus ELS); the level of significance for each planned comparison was adjusted using the Bonferroni correction for four comparisons and were taken as significant at $p < 0.01$.

***Source-level analysis.*** Experimental participants underwent MRI scanning on a 1.5-T Philips Intera system. Individual structural MRI scans were used to construct single-layer boundary element models of cortical gray matter using a watershed segmentation algorithm (FreeSurfer 4.3 software; Martinos Center for Biomedical Imaging, USA). Individual anatomical patterns were coregistered using fiducial points and approximately 60 additional scalp surface points. A grid with a 5-mm pitch was used to place the dipoles on the surface of the brain model, yielding 10,242 vertexes for each hemisphere. Sources were localized using data from both axial magnetometers and planar gradiometers. Source localization was performed using a cortical surface-constrained minimum norm estimate based on the L2 norm (unsigned) implemented in the MNE-Python software package [Gramfort et al., 2013].

The noise covariance matrix was calculated for each subject in the interval from –500 msec to –50 msec before stimulus presentation in each trial. The noise covariance matrix and forward operator were combined into a linear inverse operator using a minimum norm estimator based on the L2-norm constrained to the cortical surface (unsigned) implemented in the MNE software package. Source scores were morphed onto the standard MNI brain using the MNE surface-based normalization procedure. The activation time series in source space was analyzed by decimating the data to 200 samples per second.

First, for each time window analyzed, the cortical regions mediating the learning effect were identified. Paired *t* tests for the ELS versus LLS contrast were performed for activation, averaged across all samples of the analysis time window, in each vertex separately. Correction for multiple comparisons used the same statistical procedure as at the sensor level, but for the entire set of cortical surface vertexes instead of MEG channels. Cortical ROIs were defined as clusters of contiguous significant vertexes. Only clusters containing at least 30 cortical vertexes were considered. Results are presented with uncorrected vertex thresholds ($p < 0.05$) [Gross et al., 2013], as well as with FDR correction for the number of vertexes.

These cortical regions were then used to analyze the temporal dynamics of activation for the ELS and LLS conditions. Activation time series were constructed for each vertex independently and then averaged across adjacent vertexes within each ROI. The influence of the latency and duration of the learning effect on activation of the corresponding cortical regions were assessed by evaluating differences between the ELS and LLS conditions using the *t* test, with FDR correction for multiple comparisons for the number of time points.

**Results.** ***Behavioral indicators.*** During active operant learning, participants successfully learned to perform a task of associating eight pseudowords with the movement of specific limbs or not to make a movement. As early as in active block 1 (the active learning block), the cumulative mean proportion of correct responses by subjects was 68.0 ± 6.2% (Table 2), which was significantly different from the random level ($p = 0.02$). The probability of a correct response increased significantly over the course of training within a given block. Figure 2 shows numbers of correct responses depending on trial number at the early stage of ELS training at the group level (Fig. 2, *a*, *c*) and for individual participants (Fig. 2, *b*). The plots clearly show a general trend towards continuous improvement in task performance. The number of implementations required to achieve the learning criterion varied across participants, from 74 to 480, which corresponded to an active learning duration of 6–40 min.

In active block 2, i.e., at the stage of active execution, all participants showed almost the maximum possible results in completing the task (the average percentage of correct responses was 96.4 ± 4.0%, $p < 0.001$). Thus, the participants evidently successfully learned the relationship between each of the eight auditory cues and the corresponding action or inaction (Fig. 2, *d*).

There were no statistically significant differences in task performance accuracy between MP and NMP trials, ei-

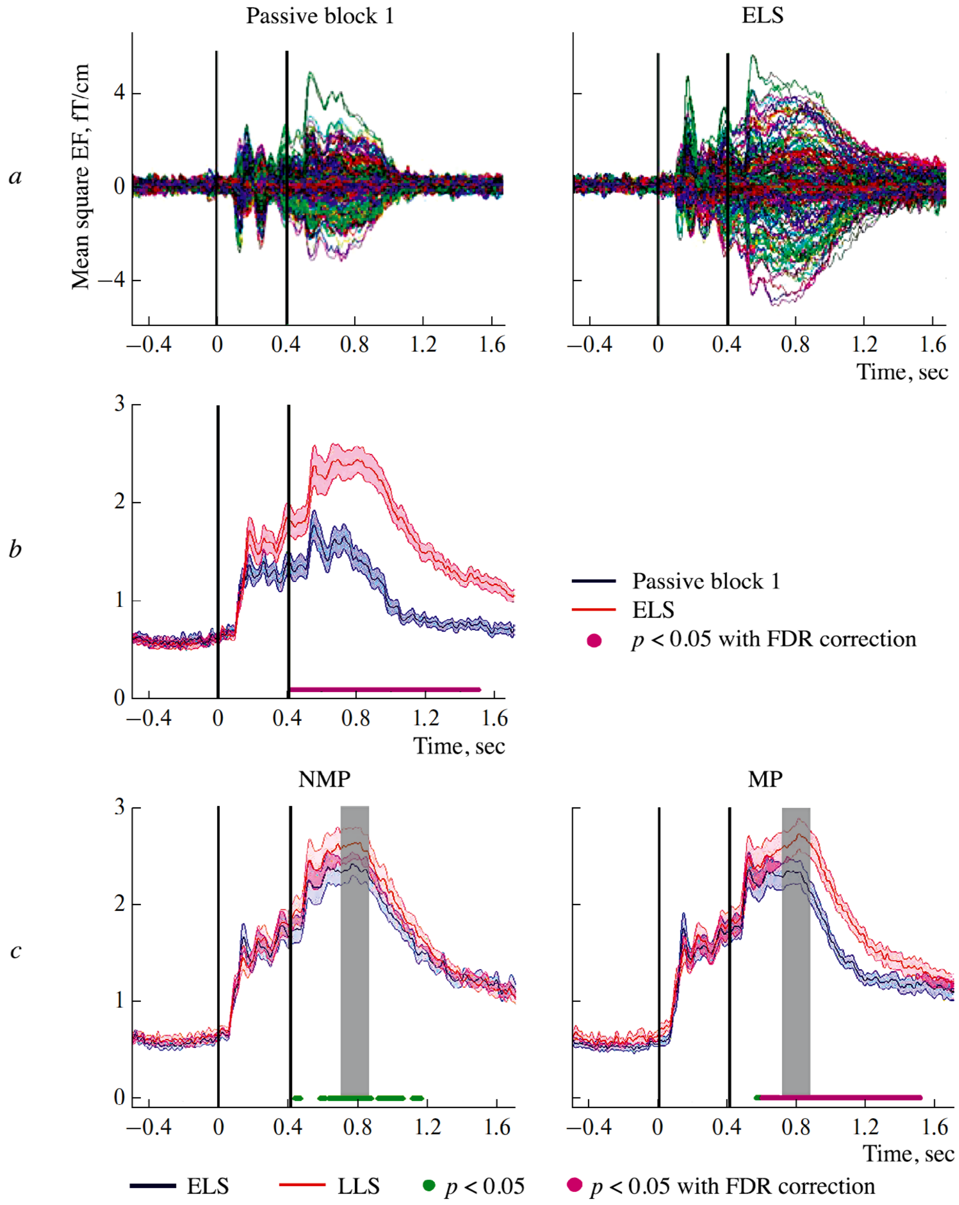

Fig. 3. Influence of performing an associative task and learning on the dynamics of EF in response to auditory pseudowords. *a*) Plots of the root mean square EF for each sensor during passive listening before training (left) and at the early stage of ELS training, NMP trials (right) only. Each line shows the dynamics of the evoked field on a separate combined gradiometer. *b*) Plots of global root mean square EF during passive listening before training and ELS, NMP trials only. *c*) Plots of global root mean square EF for the early and advanced stages of task learning (ELS and LLS, respectively). Trials in which motor reactions were not performed (NMP, at left) and those in which motor reactions were performed (MP, at right) are shown separately. Shading along each graph indicates the corresponding 95% confidence interval. The horizontal axis is time (sec) relative to the beginning of the stimulus; the vertical axis is the amplitude of the root mean square EF, fT/cm. Significant differences are indicated below the plots (two-tailed *t* test, $p < 0.05$, without correction and with FDR correction for multiple comparisons across all time points). Vertical solid lines indicate the start time of pseudoword stimulus presentation (0 sec) and the disambiguation point (0.410 sec). The gray box shows the 100-msec interval centered on the peak of the evoked field (see text for explanation).

ther at the early stage of ELS training (67.3 ± 9.8 and 69.5 ± 5.5% for MP and NMP, respectively, $t(23) = -0.95$, $p > 0.05$) or at the advanced stage of learning (96.4 ± 3.6 and 97.2 ± 4.4% for MP and NMP, respectively, $t(23) = -1.31$, $p > 0.05$).

Subjects' reaction times in MP trials were on average longer at the early stage of training than at the advanced stage of training (ELS 1492.5 ± 101.1 msec; LLS: 1352.9 ± 116.3; $t(1, 23) = 5.91$; $p < 0.0001$). Thus, as expected, the decision to perform a motor reaction in response to a stimulus was facilitated over the course of training. It is of note that even in active block 2, i.e., during active performance, a further reduction in the latency of the motor response was observed, which was confirmed by a significant negative regression between trial number and reaction time ($R^2 = -0.26$; $p < 0.001$) (Fig. 2, *e*). Thus, the auditory-motor

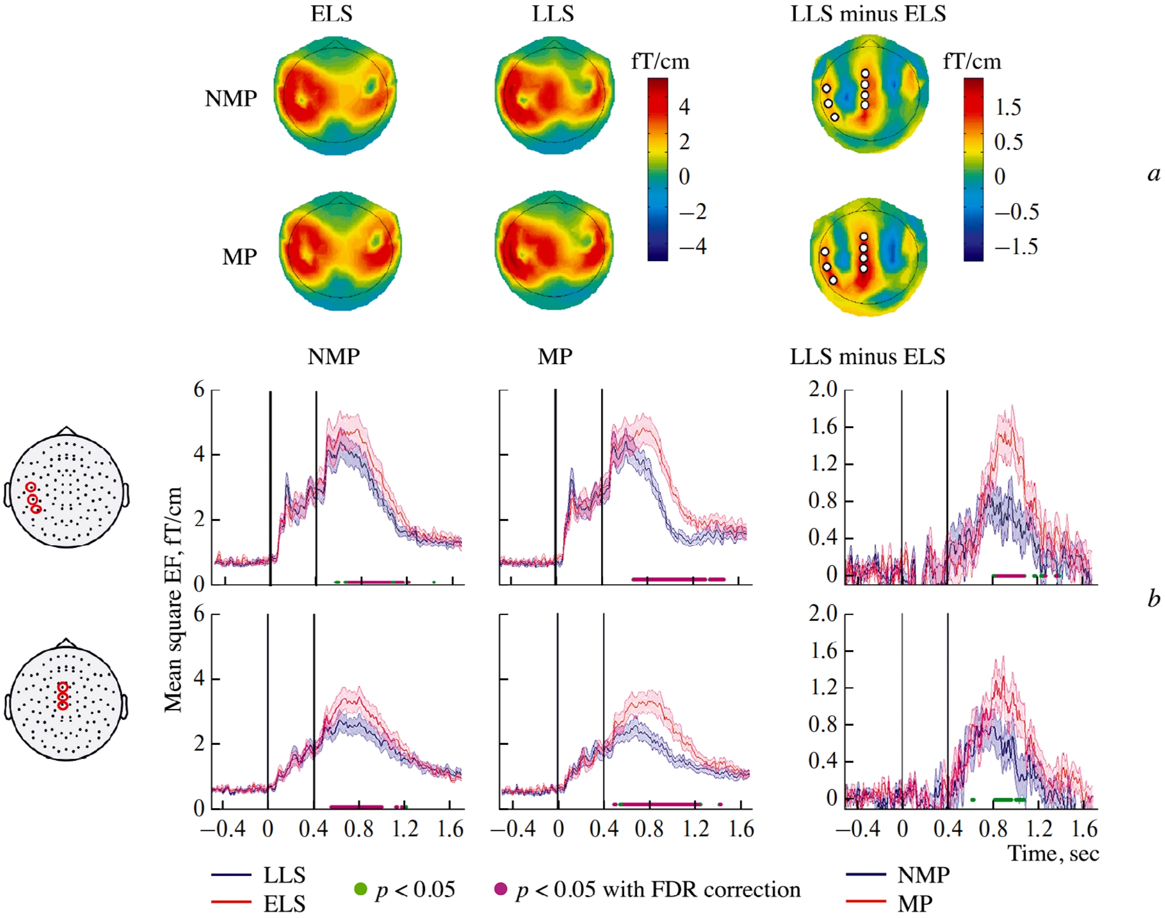

Fig. 4. Spatial maxima and duration of the learning effect (LLS > ELS contrast) of the global root-mean-square EF in MP and NMP trials. *a*) Topographic maps of the global mean square EF for NMP (top row) and MP (bottom row) trials in ELS and LLS conditions (left and middle panels), as well as for the difference between LLS and ELS (right panel), averaging over the interval 730–830 msec from the beginning of stimulus presentation. In the right panel, circles indicate the locations of the combined gradiometers at which the learning effect was significant after FDR correction for multiple comparisons. *b*) Plots of the root-mean-square EF for the lateral and medial clusters (shown in the diagram of the location of MEG sensors in the insets at left), for the ELS and LLS conditions, separately for NMP and MP trials (left and middle panels), as well as difference values (LLS minus ELS) for the NMP and MP trials. All other designations as Fig. 3.

association was further strengthened at the advanced stage of training.

***MEG analysis at the sensor level.*** *Task effect*. As a first step, we compared evoked responses to pseudowords early in training with a passive condition in which the participant listened to the same auditory stimuli without any specific task, i.e., during passive block 1 (Fig. 3, *a*). As participants did not perform any movements in the passive condition, comparability was ensured by including only trials from the NMP condition from the active block in this analysis.

Comparison of the dynamics of root mean square values of EF between the two conditions (Fig. 3, *b*) revealed a significant increase in the response during active learning, starting from approximately 500 msec from the beginning of stimulus presentation. If, in the passive condition, EF returned to the initial level by 1200 msec after the start of stimulus presentation, then during active learning the elevation persisted for much longer (to at least until 1500 msec after the start of the stimulus).

The most direct explanation for the greater strength and duration of the auditory neural response in the ELS compared to the passive state may be the increased load on attention and memory during task performance. If the role of attention is to facilitate the acquisition and memorization of stimulus-result associations, then it is logical to suppose that the amount of attention paid to auditory stimuli will be greatest early in learning [Pearce and Hall, 1980; Pearce and Mackintosh, 2010]. Following the same logic, one would expect that the effect of increased attention on the evoked response should begin to decrease as the rules of the task are learned. In contrast to this suggestion, our hypothesis – that neural representations during associative learning are prolonged – leads to the opposite prediction. Therefore, to separate the putative contribution of active learning from the contribution of attention, we next compared evoked responses between the ELS and LLS conditions.

*Learning effect*. Figure 3, *c* shows the difference between the root-mean-square values of EF for the ELS and LLS con-

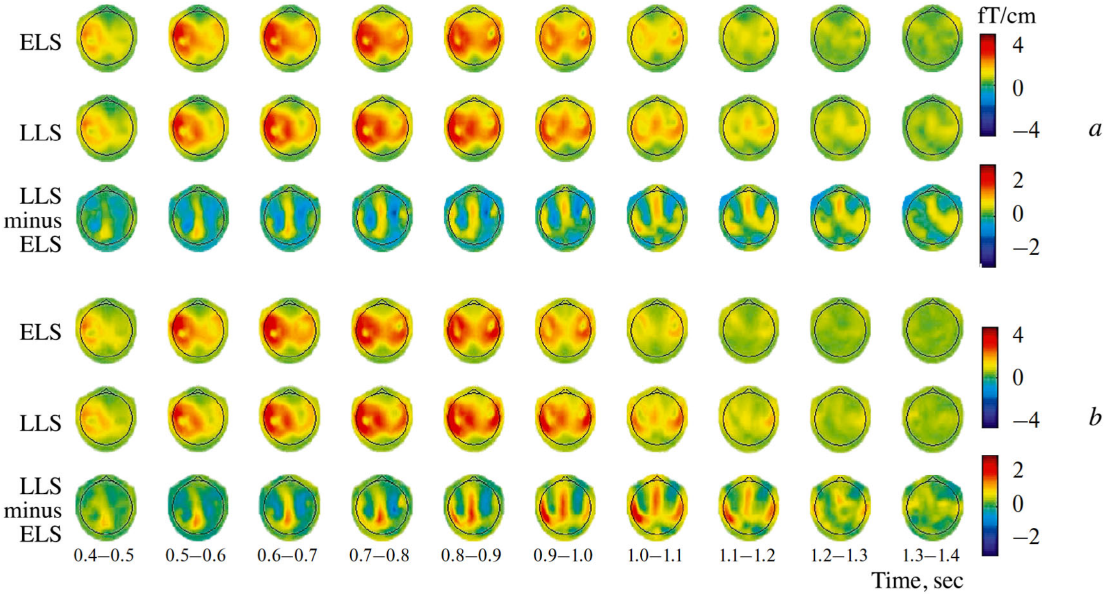

Fig. 5. Series of topographical maps of global mean square EF for NMP and MP trials. Each topographic map represents relative amplitude values averaged over time points in successive intervals indicated beneath figures. The upper and lower panels correspond to NMP (*a*) and MP (*b*) trials, respectively. In each panel, the top row corresponds to the ELS condition, the middle row to the LLS condition, and the bottom row to the difference between the LLS and ELS conditions.

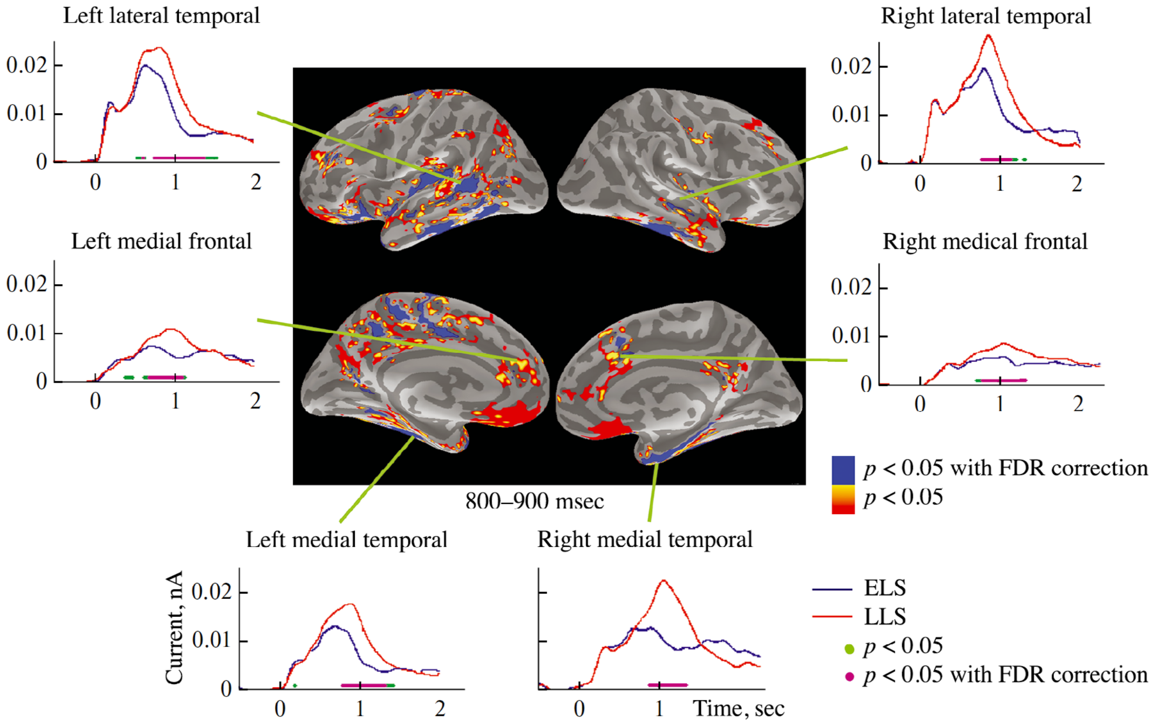

Fig. 6. Localization of the sources of the learning effect for the evoked neuromagnetic response in MP trials. The central panel shows cortical sources showing significant learning effects (LLS > ELS in the 800–900 msec post-stimulus onset time window, without and with FDR correction for the number of vertexes ($q < 0.05$). These areas were taken as regions of interest for further analysis. For clarity, areas showing a similar effect at a significance level of $p < 0.05$ (uncorrected) are also shown. The adjacent panels show plots of the dynamics of the average current in sources (without sign) from five areas of interest, for the ELS and LLS conditions. Significant differences in LLS > ELS in the plots ($p < 0.05$, uncorrected) are noted if they appear at at least 20 consecutive time points.

ditions, for MP and NMP trials separately. The responses recorded consisted of several initial short peaks followed by a large, broad peak with a latency of approximately 800 msec from stimulus onset. To assess whether learning influences auditory processing of the stimuli presented, we first examined the auditory evoked response at its maximum strength.

This was done by averaging the ELS and LLS conditions (including MP and NMP trials), which showed that the auditory evoked response in the combined data peaked at 780 ± 53 msec after stimulus onset. Given that the disambiguation point was 410 msec from stimulus onset (see Fig. 1), the peak latency of the auditory evoked response corresponded to the semantic N400 EEG and MEG components [Kutas and Federmeier, 2011; O'Rourke and Holcomb, 2002].

We next studied how the peak value of the auditory response varied across experimental conditions. For this purpose, root mean square EF were averaged over a 100-msec time interval centered on the response maximum noted above (730–830 msec from the onset of stimulus presentation). Using the resultant values, we compared the ELS and LLS conditions in terms of the types of trials of MP and NMP separately (Fig. 4, *a*).

During the peak of the auditory response, the topographies of the differential effect caused by learning were similar for MP and NMP trials: two spatial clusters were identified for both types of trials, located approximately above the left temporal cortex and the midline cortex (significant sensors are highlighted, $p < 0.05$, FDR-corr.) (Fig. 4, *a*), right panel). As shown in this illustration, enhancement in both spatial clusters was stronger for pseudowords which became associated with movements (MP) than for those which did not acquire such an association (NMP) (Fig. 4, *a*, right panel).

Sequential maps of the topography of evoked fields in the ELS and LLS conditions (Fig. 5) showed that this effect was not limited to the time period of the peak of the response, but rather represented a long-term general shift in both spatial clusters, which was particularly noticeable for MP trials.

The significance of the visible change towards a long-term stable neural response to pseudowords after they acquired the meaning of action words was tested statistically by plotting the time dynamics of gradiometer signals averaged over the sensors of the left temporal cluster and the medial cluster (Fig. 4, *b*). In fact, the statistical difference in EF between the ELS and LLS conditions continued in time significantly to the right-hand side of the peak.

For each cluster, we then calculated the mean square values of the EF in four consecutive 150-msec time intervals after the peak, for each type of trial and condition separately. The results were studied by repeated measures analysis of variance, with the factors Stage of Learning (ELS and LLS), Type of trial (MP and NMP), Topography (left temporal and medial clusters), and Time (850–1000, 1000–1150, 1150–1300, and 1300–1450 msec after stimulus onset).

A significant Stage of learning × Type of trial interaction ($F(1,23) = 23.39$; $p < 0.0001$; partial $\eta^2 = 0.5$) produced an increase in the overall strength of sustained learning-induced activation in MP compared to NMP through the whole of the time window from the peak and to its right. Regardless of the type of implementation, the learning effect weakened over time, i.e., it became less marked in the more distant time points of the neural response (Learning Stage × Time ($F(3, 69) = 20.22$; $p < 0.0001$; partial $\eta^2 = 0.47$)).

Particularly important for the hypothesis being tested was that the significant effect of learning (the ELS vs. LLS contrast) was still present in MP trials for the last two time intervals preceding the motor action (3rd interval: $F(1,23) =$ $= 24.84$; $p < 0.0001$; 4th interval: $F(1,23) = 14.54$; $p < 0.01$ with Bonferroni correction). The learning effect was not significantly different from zero in the last two time intervals in NMP trials (3rd interval: $F(1,23) = 1.25$; $p = 0.27$ without correction; 4th interval: $F(1,23) = 0.15$; $p = 0.70$ without correction). Additional analysis of variance, run for the last 4th time interval, confirmed a significant predominance of MP trials over NMP trials in terms of the duration of the learning effect (interaction of the Learning stage × Type of implementation factors, $F(1,23) = 14.67$; $p = 0.0009$; partial $\eta^2 = 0.39$).

Thus, both at and after the maximum response, the auditory response was significantly increased after training – especially in those trials in which participants made a movement in response to a pseudoword.

***Source-level analysis of MEG.*** The cerebral localization of the learning effects as demonstrated statistically in sensor space was then assessed by source localization analysis. This analysis included only MP trials in which movements were performed and which, accordingly, were the focus of this study. Cortical sources were localized in the time interval between 800 and 900 msec after the onset of the stimulus, where at the sensor level we observed the greatest learning effect in MP trials (Fig. 4). In support of the sensory topography analysis, source-level analysis showed that learning predominantly modulated areas of the lateral and medial surfaces of the left and right temporal lobes, as well as the posterior portion of the medial frontal regions and the adjacent cingulate sulcus (Fig. 6).

The contrast between the ELS and LLS conditions allowed several significant clusters of cortical sources to be identified ($p < 0.05$, FDR-corrected), with peak differences located in the left and right superior temporal sulcus, left supramarginal gyrus, left and right inferior temporal gyrus, left and right fusiform/parahippocampal sulcus, and posterior part of the left cingulate sulcus/middle superior frontal gyrus. The learning effect was evident in both hemispheres, but was more marked in the left hemisphere, which is also consistent with the results of topographic analysis at the sensor level (Fig. 4). The contribution of the temporal and parietal lobes to learning-induced activation was consistent with the classic map of brain regions involved in language comprehension in general [Friederici et al., 2017] and in the semantic N400 effect in particular [Van Petten and Luka, 2006]. However, our data also suggest the involvement of a fairly wide area of the medial-frontal neocortex.

To gain further insight into the time course of differences between ELS and LLS in MP trials, we analyzed the dynamics of learning-induced changes in activation during the post-stimulus interval for the following clusters of cortical sources in both hemispheres: the lateral temporal areas (superior temporal sulcus and superior temporal gyrus, STS/STG), the supplementary and presupplementary motor areas (SMA and pre-SMA), and the fusiform/parahippocampal gyri (FFG/PHG) (Fig. 6). Source current time series were extracted and averaged across all vertexes of each cortical cluster separately, and comparisons were then made between the ELS and LLS conditions using the *t* test at each time point in the post-stimulus interval (with the FDR correction for the number of time points).

Our source-level results were broadly similar to those obtained at the sensor level, but yielded more detailed information about the onset and displacement of learning-induced activity in the cortical regions of interest. Plots of activation dynamics for LLS began to differ significantly from those for ELS, first in the left cortical areas (STS and SMA/preSMA), and then in the symmetrical areas of the right hemisphere and the medial temporal area (FFG/PHG). For the SMA/preSMA regions, the learning effect mainly coincided with the response maximum (from 500–700 to 1200 msec after stimulus onset). In contrast, learning-induced activation persisted longer in the lateral and medial temporal lobes (STS bilateral, FFG/PHG left), until approximately the mean time of movement onset (i.e., 1400–1450 msec after stimulus onset).

In summary, our results suggest that when auditory pseudowords acquired associations with a specific movement through active learning, they began to produce a stronger and longer-lasting evoked response to the stimulus. This learning effect was stronger and more prolonged for auditory stimuli instructing the body to move a limb than for those instructing it to refrain from moving. The cortical areas most affected by learning in MP trials were the superior temporal (STS) and fusiform/parahippocampal gyri (FFG/PHG) of the left and, to a lesser extent, the right temporal lobe, as well as areas of the medial frontal structures. In the temporal regions of both hemispheres, learning-related modulations persisted until the end of the delay period between the stimulus and onset of movement.

**Discussion.** The objective of this study was to identify the effect of increased and prolonged activation of the temporal cortex during the development of associations between auditory-verbal stimuli and movement. We did indeed find an effect.

Even at the early stage of learning auditory pseudowords – as compared with passive listening to them – an increase and prolongation of the N400m lexical-semantic component was observed, with a maximum effect approximately 400–450 msec after the point of pseudoword disambiguation.

A possible explanation for the effect consisting of prolongation of auditory-verbal activation found here could be that the subjects, due to fatigue or other reasons, began to spend more time recognizing stimuli by the end of the experiment. However, this explanation is contradicted by reductions in reaction time, both between active blocks and within each block, as well as an increase in the proportion of correct responses.

An N400 wave lasting quite long after the peak – similar to that observed in our study – has previously been recorded for both verbal and nonverbal stimuli in the visual modality [Deacon and Shelley-Tremblay, 2000; Erlbeck et al., 2014; Kutas and Federmeier, 2011], especially for tasks involving the active retention of a stimulus representation in short-term memory, such as the delayed matching-to-sample task [Pinal et al., 2014] or the task of encoding letters in Morse code [Lang et al., 1987].

Studies of a delayed matching-to-sample task in monkeys observed sustained firing of neurons in the inferior temporal cortex during the delay between the target visual stimulus and a well-learned behavioral response. This appeared to reflect the active maintenance of internal representations of the stimulus as required for the upcoming behavior [Takeda et al., 2005]. Taking the literature data into account, we hypothesized that the prolongation of N400m to auditory pseudowords at an early stage of learning is the result of increased load on working memory – the intentional retention of a pseudoword representation in short-term memory.

However, such an interpretation is insufficient to explain the changes in EF seen in our work during the learning process. Throughout the training period, the pseudoword-action association task required both focused attention and retention of stimuli in memory. However, as learning progresses, the association of stimulus with movement becomes more automatic, such that the load on working memory and attention decreases [Pearce and Mackintosh, 2010], which in turn should reduce the neural activation associated with working memory/attention (see, for example, [Jensen and Tesche, 2002]). Thus, these processes by themselves could hardly provide the increase and prolongation of stable neural activation identified here, especially marked at the advanced stage of learning – when errors practically disappeared and reaction time decreased significantly, which clearly indicates a significant degree of automation of reactions to stimuli.

In contrast, the above result fits well with the retrospective activation hypothesis. Indeed, only when prior learning experiences could be integrated did we observe that the neural response to newly acquired action pseudowords (which were consistently and uniquely paired with movements of a specific body part) was maintained until the onset of the expected movement (Figs. 4, *b*, 5, and 6). Considering that the learning effect for pseudowords not associated with movement (NMP) decreased sharply after the maximum of the auditory response and completely disappeared in the late part of the neural response (Fig. 4), we conclude that prolongation of the N400 wave was characteristic of those pseudowords that became predictable cues for movement selection, preparation, and execution. Appearing in anticipation of motor actions completely determined by the auditory stimulus, the retrospective increase and prolongation of activity could be a consequence mainly of the fact that in the advanced stage of learning (LLS), in contrast to the early stage of learning (ELS), participants had already established for themselves the correspondence between stimuli and responses, such that the actions performed were assessed by the participants as "correct" as early as at the stage of initiation and execution of the movement. A similar increase in sustained neuronal activity was observed in the primate prefrontal cortex when monkeys learned, through trial and error, arbitrary associations between each of two pictures and eye movements to the left or right [Histed et al., 2009].

However, and very important for the retrospective activation hypothesis, our study demonstrated learning-induced sustained activity in the classical "language areas" of the left and, to a lesser extent, the right temporal lobe (Fig. 6), which are involved in the phonological and lexical-semantic processing of real words [Kutas and Federmeier, 2011; McCarthy et al., 1995; Smith et al., 1986; Travis et al., 2012]. This suggests that speech processing resources are mobilized during the pre-movement delay period, primarily for those pseudowords which have temporarily acquired the meanings of action words. Given that the prefrontal cortex contains neuronal populations which encode sensory representations, motor representations, and reward representations (see [Histed et al., 2009]), this structure, via descending projections, may play a key role in this general mechanism of active learning of arbitrary sensory-motor associations.

However, the effect we found was not limited only to auditory-verbal representations. In addition to the temporal auditory-speech cortex, the supplementary motor and pre-supplementary motor cortex, as well as the motor areas of the cingulate cortex, i.e., areas typically involved in motor programming [Picard and Strick, 2001] also showed increased neural responses to pseudowords at the advanced stage of learning (Fig. 6). Interestingly, an fMRI study reported by Postle et al. [2008] showed that activation of the pre-supplementary motor cortex was significantly greater during understanding of the meanings of words specifically correlated with specific actions as compared with other words; the authors' view was that this activation may reflect an association between words and the initiation of a movement program.

It is important to note that the activation of the supplementary and pre-supplementary motor cortex seen here in response to the stimulus was not long enough to cause initiation of the corresponding movement as such (Fig. 6). Instead, the appearance of motor cortex activation in the classic N400m window (400 msec after the disambiguation point) suggests that this structure may be involved in the lexical-semantic retrieval/encoding of auditory action pseudowords as a neural representation of newly learned motor associations. However, the lack of SMA activation during passive listening to the same newly-learned action pseudowords [Razorenova et al., 2020] suggests that after a brief period of active learning, such auditory-motor associative correspondences are still fragile and require allocation of attentional and working memory resources in order to be detected in the neural MEG signal in response to a stimulus.

Overall, our results indicate that following the acquisition of an association between an auditory pseudoword and a predicted action, the retrieval of lexical-semantic knowledge stored in the temporal cortex is triggered by the pseudoword presented.

The present work provided the opportunity to study the dynamics of evoked brain responses only within the duration of the experiment, i.e., a period of about 1.5–2 hours. The actual duration of the effect identified here remains unknown, and discovering the answer to this question may be a promising direction for further research.

**Conclusions.** Our results provide the first evidence that the adult brain establishes new associations by relying on a mechanism allowing it to cover the whole time gap between the sounding of a word and the associated action. This is achieved by prolonging stimulus-evoked cerebral auditory-verbal activation. In this way, conditions are created for the implementation of Hebbian plasticity, that is, long-term synaptic rearrangements in neural ensembles, which is based on the coincidence of activity in time.

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