A causal role of sensory cortices in behavioral benefits of ‘learning by doing’

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Abstract

Despite a rise in the use of “learning by doing” pedagogical methods in praxis, little is known as to why these methods may improve learning outcomes. This is surprising given that an increased mechanistic knowledge of learning by doing-based improvements has the potential to speed up the development of evidence-based teaching practices. Here we use neuroscience methods and a gesture-enriched foreign language (L2) vocabulary learning paradigm to adjudicate between opposing predictions of two neuroscientific learning theories. We demonstrate that sensory brain regions associated with the processing of gesture-related stimulus information causally contribute to performance benefits following gesture-enriched L2 vocabulary learning. Sensory brain responses benefitted both short- and long-term learning outcomes, as well as the learning of both concrete and abstract words. These findings suggest that responses within specialized visual sensory cortices precipitate sensorimotor-based learning benefits. Such a mechanism could play a role in comparatively effortless native language learning and may be key for accelerating L2 proficiency in adults.
Native language (L1) learning proceeds effortlessly during infancy and is driven by extensive sensorimotor interaction with caregivers and the environment\textsuperscript{1,2}. Foreign language (L2) vocabulary learning by adults, however, is effortful and time-consuming, and typically relies on unisensory material such as written word lists or audio recordings\textsuperscript{3-5}. As many have experienced, word lists must be relearned often in order to build up robust memory representations for new vocabulary. More recent learning by doing-based approaches, contrast with these techniques\textsuperscript{6}. Though initially viewed as unconventional, principles of learning by doing have shifted from the periphery of educational science toward its center over the past few decades\textsuperscript{7}. The goal of learning by doing is to engage in activity that encourages reflection upon the learning material\textsuperscript{8}. Here we refer to learning by doing strategies as sensorimotor-enriched learning. Quantitative studies of sensorimotor-enriched learning are by and large lacking; one recent analysis suggested that sensorimotor-enriched teaching methods boosted undergraduate test performance in science, engineering, and mathematics courses compared to sensory-only teaching methods\textsuperscript{9}. Sensorimotor-enriched pedagogical approaches to L2 learning such as the performance of iconic gestures during vocabulary learning have been suggested as a means of better approximating L1-like learning experiences and potentially facilitating language acquisition\textsuperscript{10}. Iconic gestures occur spontaneously during L1 production in adults\textsuperscript{11}, and are used by young children to communicate during language development\textsuperscript{12}. The performance of iconic gestures during the auditory presentation of both L1\textsuperscript{13} and L2\textsuperscript{14} words boosts learning outcomes compared to commonly-practiced auditory- or visual-only vocabulary learning strategies in the laboratory environment. Pioneering translational studies additionally suggest that beneficial effects of gesture enrichment may also carry over to the classroom\textsuperscript{15}.

The mechanisms underlying enhanced memory for sensorimotor-enriched stimuli remain elusive. It has been suggested that the presence of complementary sensory or motor information during learning (“enrichment”) lays down motoric memory traces\textsuperscript{16,17} as well as multisensory memory traces\textsuperscript{1,18,19}, establishing a greater number of routes for successful memory retrieval. Investigations of brain responses to trained sensorimotor stimuli are in agreement with these accounts. For example, children demonstrate increased motor cortex responses when viewing letters that they have previously been taught to write, compared to letters that they have been taught to recognize visually\textsuperscript{20}. Similarly, the translation of auditorily-presented L2 words that have previously been taught using gestures elicits responses within pre-/motor cortices in adults\textsuperscript{21}. Auditory L2 translation also elicits specialized visual cortical responses: Whereas the biological motion area of the superior temporal sulcus (bmSTS)
becomes engaged following gesture-enriched vocabulary learning, the lateral occipital complex (LOC) is engaged following picture-enriched vocabulary learning. Uncovering whether multisensory and motor memory traces mediate behavioral benefits of sensorimotor-enriched learning is essential for the effective development of evidence-based teaching methods. On one hand, responses to unimodal stimuli within specialized sensory and motor brain regions following sensorimotor-enriched learning may be viewed as epiphenomenal, a view taken by reactivation-based theories of multisensory learning. Reactivation theories suppose that sensory and motor brain responses engender a mere representation of the memorized stimulus, and therefore serve effectively no functional role in memory recognition. Beneficial effects of learning could then be relegated to the arousing influence of sensorimotor enrichment on learning, and efforts to develop novel teaching strategies could be geared towards that aspect of enrichment. On the other hand, sensory and motor brain responses to previously-learned items may directly benefit recognition processes by increasing recognition speed and accuracy. The predictive coding theory of multisensory learning takes this approach by proposing that sensory and motor cortices build up sensorimotor (e.g., visuomotor) forward models during perception that predict or simulate missing input, which functionally benefit behavioral learning outcomes. If sensory and motor brain responses during unimodal stimulus presentation are functionally relevant for learning outcomes, teaching techniques could be optimized to target specific sensory structures that underlie task performance. Thus, the first aim of the current study was to adjudicate between reactivation-based and predictive coding theories of multisensory learning.

Investigating the neural bases of sensorimotor-induced memory enhancement will provide critical insight into the role of sensory cortices in memory, a topic that is currently intensely debated. Human memory is often partitioned into procedural memory, which is anchored in sensory and motor systems, and declarative memory for facts and events. Though memory for vocabulary has been construed traditionally as a form of declarative memory, sensorimotor-enriched training may anchor L2 vocabulary representations in procedural memory systems. Procedural memories are known to decay less rapidly than newly-learned declarative memories and are less vulnerable to interference following stabilization. Therefore, the second aim of the current study was to evaluate the functional role of sensory brain responses in learning outcomes over an extended time period (> 5 months post-training). Given the temporal robustness of sensorimotor-based neural representations, we expected that multisensory brain responses would boost learning outcomes over extended post-training durations.
A potentially limiting factor in the success of sensorimotor-enriched approaches to L2 vocabulary learning may arise from the conceptual perceptibility of word referents. Conceptual perceptibility refers to the extent to which referents can be perceived by the body’s sensory systems (e.g., tangibility, visibility\(^40\)). The referent of the concrete noun *ball*, for example, is highly tangible and can be iconically represented by using one’s arms to throw an imaginary ball. Referents of other words, such as the abstract nouns *mentality* or *theory* are less tangible and are therefore more difficult to convey using gestures or pictures. Abstract words are more difficult for learners to acquire than concrete words, both in L1\(^41\) and L2\(^42\). One explanation for the faster acquisition of concrete words is that their referents possess intrinsic associations with the body’s sensory and motor systems\(^43,44\). Abstract words may instead be represented introspectively via internal states\(^45\), through metaphor\(^46\), or based on the context of specific situations\(^41\). Given that concrete and abstract L1 words differ in terms of their intrinsic sensorimotor associations, the third aim of the current study was to address whether sensory brain regions differentially contribute to gesture-enriched learning benefits for these word types.

Though functional neuroimaging has contributed much to our understanding of interactions between information arising from distinct sensory modalities, neuroimaging techniques are limited to demonstrations of correlational rather than causal effects\(^47\). Here, we use transcranial magnetic stimulation (TMS) to test whether or not brain regions that are engaged during sensorimotor-enriched learning causally contribute to its beneficial behavioral effects. During TMS, small magnetic fields are applied non-invasively to the scalp, targeting a specific brain area. The magnetic fields induce electrical currents in the underlying brain tissue, transiently interfering with processing in that specific area\(^48\). If the stimulated region is causally relevant for an ongoing task, then an observable behavioral effect, often an increase in response latencies, can be induced\(^49-53\). The use of TMS is key for making causal claims regarding the role of specialized sensory and motor areas in behavioral benefits of sensorimotor-enriched learning, and cannot be substituted by behavioral, functional magnetic resonance imaging (fMRI), or other neuroscience measurements that fall prey to pitfalls of causal inference\(^54\).

In the current study, adult learners were trained on 90 novel L2 words and their L1 translations over 4 consecutive days (Fig. 1a). L2 vocabulary (concrete and abstract nouns, Table 1) was learned in two conditions. In a gesture-enriched learning condition, individuals viewed and performed gestures while L2 words were presented auditorily (gesture enrichment). In a control condition, individuals viewed pictures while L2 words were presented auditorily (picture enrichment) (Fig. 1b). Gestures and pictures were congruent with word meanings. We then used TMS to target the bmSTS, a region implicated in visual perception of biological movements\(^55,56\) that
has previously correlated with behavioral benefits of gesture enrichment, but not with picture enrichment, in an L2 translation task\textsuperscript{22}. TMS was applied to the bilateral bmSTS while participants translated auditorily-presented L2 words into L1 at two time points: 5 days and 5 months following the start of L2 training. Participants did not perform gestures or view pictures during the TMS task. A within-participants control condition was included in each TMS session by applying both effective and sham TMS to the bilateral bmSTS (Fig. 1c).

Figure 1 | Experimental procedure and design. a, Participants learned foreign language (L2) vocabulary over four consecutive days (‘learn’) in groups to emulate a classroom setting. Free recall and translation tests (‘test’) were administered on days 2 through 4. Transcranial magnetic stimulation (TMS) sessions occurred during day 5 and month 5. b, In both gesture and picture learning conditions, participants heard an L2 word, followed by the translation in their native language (L1) and a repetition of the L2 word. Videos of iconic gestures and pictures accompanied L2 words in gesture and picture trials, respectively. Participants performed the gesture along with the video during its repetition. c, During both TMS sessions (day 5 and month 5), two TMS coils targeted the bilateral biological motion superior temporal sulcus (bmSTS) using stereotactic neuronavigation based on individual structural brain scans. Two additional coils...
generated ineffective placebo stimulation (i.e., sham TMS) and were positioned on top of the bmSTS coils at an angle of 90°. During each TMS session, participants heard the L2 words that they had learned during the 4-day training and then selected the L1 translation by button press from a list of options presented on a screen. L1 words were presented in German. Trains of seven TMS pulses at 10 Hz were delivered 50 ms following each L2 word onset. Trials with effective and sham TMS alternated in blocks. Note that participants additionally pressed a button as soon as the L1 translation came to their mind following each auditorily-presented L2 word (not shown, see methods for more details).

We tested three main hypotheses. First, according to the predictive coding theory of multisensory learning, the application of inhibitory stimulation to the bmSTS should slow down the translation of an auditorily-presented L2 word if the word has been learned with biological motion as is the case with gestures, but not if it has been learned with pictures. In contrast, reactivation-based learning theories, which assume that reactivated areas do not play a functional role in recognition, would predict no differential effects of bmSTS stimulation on the translation of auditorily-presented L2 words. Our second hypothesis was that gesture-enriched learning would yield more temporally robust L2 memory representations compared to picture-enriched learning, because sensorimotor, procedural memories are thought to decay less quickly over time than declarative memories. We therefore expected less decay over time of memory for L2 words learned using gestures compared to L2 words learned with pictures, and additionally aimed to explore whether there were greater effects of bmSTS stimulation on the translation of L2 words learned using gestures at the later time point (5 months) compared to the earlier time point (5 days). Our third hypothesis was that bmSTS stimulation would yield similar effects on the translation of both concrete and abstract words. This prediction was based on previous results showing that sensorimotor enrichment can benefit the learning of both word types.

Results

Stimulation of the bmSTS slows the translation of gesture-enriched foreign vocabulary

Our first and primary hypothesis was that a brain region specialized in the perception of biological motion, the bmSTS, causally contributes to L2 translation following gesture-enriched L2 learning, but not picture-enriched L2 learning. We therefore first tested whether bmSTS stimulation modulated L2 translation, irrespective of testing time point. The results confirmed our hypothesis. A two-way analysis of variance (ANOVA) on response times revealed a stimulation type × learning condition interaction ($F_{1,21} = 11.58, P = .002$, two-tailed, $\eta_p^2 = .36$). Tukey’s HSD
post-hoc tests revealed that response times for words that had been learned with gesture enrichment – but not picture enrichment – were significantly delayed when TMS was applied to the bmSTS compared to sham stimulation \((P = .005, \text{Hedge’s } g = .33)\). This indicates that perturbation of a brain area related to biological motion slowed the translation of L2 words that had been learned with gestures, but not of L2 words learned with pictures (Fig. 2).

![Figure 2](image)

**Figure 2 | Effects of bmSTS stimulation on L2 translation.** Bilateral bmSTS stimulation slowed the translation of L2 vocabulary learned using gestures compared to L2 vocabulary learned using pictures. The mean of each condition across time points (5 days and 5 months following the start of learning) is shown \((n = 22 \text{ participants})\). Error bars represent one standard error of the mean. *\(P < .05\), **\(P < .01\).

In a control analysis, we tested whether differences in response times under effective stimulation compared to sham stimulation conditions could be due to tradeoffs between translation speed and accuracy. Correct response times in the multiple choice translation task were compared with accuracy (percent correct) for each learning condition, stimulation condition, and time point. Response times correlated negatively with translation accuracy: Slower responses were associated with lower accuracy (Table 1). Correlations reached significance for all but one condition. Thus, participants did not trade speed for accuracy.
Table 1 | Speed-accuracy relationships in L2 translation. Slower response times correlated with lower translation accuracy, indicating that there was no speed-accuracy tradeoff. \(df = 20\) for all correlations.

Gesture-enriched training facilitates long-term speed and accuracy of foreign vocabulary translation

Our second hypothesis was that memory for L2 would be more temporally robust following gesture-enriched learning compared to picture-enriched learning. We first tested whether gesture-enriched learning yielded less L2 memory decay over time compared to picture-enriched learning. Changes in L2 representations over time were evaluated by comparing changes in L2 translation speed and accuracy at 5 days and 5 months following the start of learning. Only sham condition speed and accuracy measures were evaluated, in order to assess differences between gesture- and picture-enriched learning in the absence of neurostimulation.

A two-way ANOVA on changes in translation accuracy across the two testing time points (day 5 – month 5) revealed a learning type × vocabulary type interaction \((F_{1,21} = 13.84, P = .001, \text{two-tailed, } \eta^2_p = .40)\). Tukey’s HSD post-hoc tests revealed a greater decrease in translation accuracy over the 5-month interval following picture-enriched learning compared to gesture-enriched learning for concrete words only \((P = .009, \text{Hedge’s } g = .58)\). Thus, gesture-enriched representations of concrete L2 words were less susceptible to memory decay processes than audiovisually-enriched L2 representations (Fig. 3a).

A two-way ANOVA on changes in translation response time across the two testing time points (month 5 – day 5) revealed a main effect of learning condition \((F_{1,21} = 11.05, P = .003, \text{two-tailed, } \eta^2_p = .34)\). A greater increase in response times occurred over the 5-month interval following picture- enriched learning compared to gesture-enriched learning (Fig. 3b). Therefore, gesture-enriched learning benefitted translation response times more than picture-enriched learning over the long-term, indicating the robustness of gesture-enriched L2 representations in memory over a long timescale.
Figure 3 | Long-term change in accuracy and speed of L2 translation following learning. a, Performance of iconic gestures during L2 vocabulary learning resulted in less decay of concrete L2 word knowledge over a 5-month period compared to traditional audiovisual (picture) learning \((n = 22 \text{ participants})\). b, Compared to picture-enriched learning, gesture-enriched learning resulted in less of an increase in translation response times at 5 months following training \((n = 22 \text{ participants})\). Error bars represent one standard error of the mean. **\(P < .01\).

We next explored whether effects of inhibitory TMS on the translation of gesture-enriched L2 words differed across testing time points by comparing effects of TMS on translation response times at each time point (day 5 and month 5). A three-way ANOVA on response times yielded a significant three-way stimulation type \(\times\) learning condition \(\times\) time point interaction \((F_{1,21} = 10.54, P = .012, \text{ two-tailed, } \eta^2_p = .26)\). Tukey’s HSD post-hoc tests revealed a response benefit (faster responses) for gesture-enriched learning compared to picture-enriched learning under sham stimulation 5 months following learning \((P < .001, \text{ Hedge’s } g = .69)\). The application of TMS to bmSTS negated this benefit: Responses were significantly slower for the gesture condition at month 5 during TMS compared to sham stimulation \((P = .001, \text{ Hedge’s } g = .61)\). In sum, significant effects of bmSTS stimulation on translation occurred 5 months following the L2 training period (Fig. 4).
Figure 4 | Effects of bmSTS stimulation on L2 translation by time point. Effects of bmSTS stimulation occurred 5 months following learning ($n = 22$ participants). Error bars represent one standard error of the mean. *$P < .05$, **$P < .01$.

Effects of bmSTS stimulation depend on the conceptual perceptibility of learning material

Finally, we tested our third hypothesis that the disruptive effects of bmSTS stimulation would occur independent of the conceptual perceptibility of the L2 word referents (i.e., whether a word was concrete or abstract). A four-way ANOVA on translation response times yielded a significant four-way stimulation type × learning condition × time point × vocabulary type interaction ($F_{1,21} = 5.24$, $P = .033$, two-tailed, $\eta^2_p = .20$). Tukey’s HSD post-hoc tests revealed that concrete nouns paired with gestures during learning were translated significantly more slowly during bmSTS stimulation compared to sham stimulation at day 5 ($P = .05$, Hedge’s $g = .31$; Fig. 5). This comparison was not significant for abstract nouns at day 5. At month 5, however, TMS significantly slowed the translation of both L2 word types following gesture-enriched learning but not picture-enriched learning (concrete words: $P = .002$, Hedge’s $g = .44$; abstract words: $P < .001$, Hedge’s $g = .48$). This demonstrates that stimulation of the bmSTS affected the translation of the concrete gesture-enriched L2 vocabulary at the earlier time point, and the translation of both concrete and abstract gesture-enriched vocabulary at the later time point.
In line with previous literature\textsuperscript{58}, concrete L2 vocabulary was translated more accurately overall than abstract L2 vocabulary: A four-way ANOVA on translation accuracy (percent correct) confirmed a significant main effect of vocabulary type ($F_{1, 21} = 35.6, P < .001$, two-tailed, $\eta^2_p = .63$). Overall, concrete nouns were translated significantly more accurately ($M = 71.0\%$, $SE = 2.0\%$) than abstract nouns ($M = 63.2\%$, $SE = 2.2\%$).
Discussion

This is the first study to our knowledge to causally link brain responses in specialized sensory cortices to facilitative effects of sensorimotor-enriched learning. There were three main findings. First, behavioral benefits of gesture-enriched learning were caused in part by responses within a specialized visual brain area, the bmSTS; this area was causally engaged in the auditory translation of gesture-enriched L2 words but not picture-enriched L2 words. Second, memories for gesture-enriched words demonstrated less memory decay than picture-enriched words over the 5-month period following L2 training, and bmSTS integrity benefitted behavioral outcomes over the same time period. Third, bmSTS integrity benefitted the translation of both concrete and abstract L2 words, though gesture-enriched representations of abstract words within the bmSTS took longer to develop. Taken together, these findings suggest that sensorimotor-enriched training constructs strong associations between auditory L2 words and their L1 translations by way of representations arising from specific visual cortices. Robust long-term memory representations established by learning by doing pedagogical techniques may therefore be supported by task-specific, specialized sensory brain responses.

The causal relation observed between bmSTS responses and L2 translation adjudicates between influential reactivation-based and predictive coding theories of multisensory learning. The finding that brain responses in one sensory modality (e.g., visual) can improve task performance in another modality (e.g., auditory), depending on associations forged during learning, is predicted by predictive coding theories but not reactivation-based theories. The bmSTS may have supported the internal simulation of visual biological motion during the auditory translation task, thereby benefitting response times. We would expect similar effects of motor and somatosensory stimulation on the translation of gesture-enriched but not picture-enriched words (for preliminary results, see). The current study significantly advances previous fMRI findings by demonstrating the causal relevance of specialized sensory brain responses in behavioral benefits of sensorimotor-enriched learning. Critically, while both gesture-enriched and picture-enriched training involved complementary visual information, disruptive effects of bmSTS stimulation occurred only for the condition that contained stimulus information related to biological motion. Therefore, engagement of the visual bmSTS depended on prior sensorimotor experience.

The perception of familiar L1 vocabulary activates an experience-dependent network of sensory and motor areas. Reading the word “salt” in L1, for example, can trigger processing in regions of the brain related to taste, and spoken action words such as “kick” and “pick” elicit neural responses within somatotopically-related areas of the motor and premotor cortices. Some neurostimulation evidence has pointed to the functional relevance of motor areas in behavioral...
responses to L1 action words that refer specifically to body movements\textsuperscript{65}. Our findings add a fundamentally novel line of research to this previous result, because we show the causal relevance of sensory brain responses in the representation of recently-acquired L2 words, and, in particular, non-action words such as concrete and abstract nouns. L1 word recognition potentially takes into account lifelong experience with words and their perceptual associations, making it difficult to disentangle the relationship between language learning experience and sensorimotor neural responses. The use of an artificially-generated vocabulary constrained by phonotactics of an existing language in the current study permitted the control of variables related to participants’ learning experience such as frequency of vocabulary exposure, sensorimotor repetition, learning context, and conditions of recognition, as well as stimulus-related variables such as word lengths, phonological contents, functions, and speaker, and so forth. Based on the current results, unfamiliar L2 words can become associated with sensorimotor information and subsequently represented within specialized sensory cortices via sensorimotor-enriched learning. Thus, lifelong experience with words and their semantic associations is not a prerequisite for establishing representations of auditory words within visual cortices. Indeed, contributions of the bmSTS to L2 translation arose following a relatively brief period of sensorimotor-enriched L2 training. The short training period required suggests that sensory and motor elements of gesture-enriched learning experience can be integrated rapidly with vocabulary representations.

A key aspect of how information arising from distinct modalities can be integrated during learning is the information’s congruency\textsuperscript{29,66,67}. For example, the performance of iconic gestures during L2 vocabulary learning enhances memory for the vocabulary, but the performance of meaningless gestures does not\textsuperscript{14}. Similarly, concrete concepts map more easily onto gestures compared to abstract concepts\textsuperscript{42}, which are less conceptually perceptible\textsuperscript{44}. The reduced congruence between gestures and abstract concepts may have resulted in learners’ reliance on alternate short-term memory strategies for translation abstract L2 words at the earlier time point. Nevertheless, bmSTS stimulation inhibited the translation of both gesture-enriched concrete and abstract words at the later time point, consistent with the previous demonstration of greater long-term memory benefits for both word types following gesture enrichment compared to picture enrichment\textsuperscript{22}. Sensorimotor facilitation of the translation of abstract L2 nouns in adults may function by building associations between abstract concepts and perceptible sensory and motor events. The L2 translation of the word *innocence*, for example, is difficult to learn if paired simply with its native language translation. It becomes easier to learn if paired with the iconic gesture of shrugging of one’s shoulders, even though innocence is not defined as shrugging\textsuperscript{42}. From this standpoint,
sensorimotor-enriched training may be even more valuable for the learning of abstract words than other word types, as abstract words are generally more difficult to learn in both L1 and L2. Glenberg and Gallese propose that sensory and motor associations with abstract concepts build up incidentally during L1 development. Our findings show that there are mechanisms in place that could be coopted for such incidental L1 vocabulary learning to occur.

What kind of mechanism may explain the involvement of specialized sensory cortices in sensorimotor-enriched L2 learning? In order to recall the meaning of a newly-acquired L2 word, one may internally re-enact the perceptual and motor processes that were involved in learning that word. This re-enactment effectively proceduralizes memory for the vocabulary. Numerous behavioral studies support the notion that perceptual and motor processes involved in learning are re-enacted during recognition. During reading, for example, concrete nouns such as plane and soccer ball elicit upward and downward saccades, respectively, suggesting that visuomotor simulations are involved in accessing semantic knowledge (replicated in). The mechanism of sensorimotor simulation provides a link between specialized sensory brain responses and procedural memory retrieval. Procedural memories have been described as learned connections between stimuli and actions that define “how” to do something. Given the strong associations formed between actions and their sensory outcomes, memory for actions may rely on the simulation of sensory consequences of actions in addition to (or even more than) the simulation of motor representations that are used to produce those sensations. Thus, whereas idiosyncratic L2 knowledge such as the link between an L1 word and its L2 translation may be housed within declarative memory systems, the representation of L2 words within specialized visual sensory areas following sensorimotor-enriched training suggests that memory for L2 is partly embedded within procedural memory. This view is consistent with the finding that gesture-enriched L2 words elicit responses within brain areas associated with declarative memory such as the hippocampal formation, but also in sensory and motor areas tied to procedural memory. The view is also consistent with the idea that the presence of an additional dimension (e.g., visual, somatosensory) along which stimuli can be evaluated during recognition underlies the beneficial effects of learning by doing. Proceduralization of L2 semantic knowledge could also explain the greater robustness of gesture-enriched compared to picture-enriched neural L2 representations over long timescales observed in the current study.

A growing literature has reported positive effects of arousal-based interventions such as acute physical exercise, mood and emotion regulation, and even background music on memory and performance on cognitive tasks. Though effective, these arousal-based approaches do not encode associations between different features of an experience in the same way that
gestures are bound to specific stimulus information. Thus, the current results steer away from more general explanations for beneficial effects of sensorimotor-enriched learning such as increased arousal or attention. Teaching strategies may therefore be advanced by establishing congruent links between new information and complementary multisensory enrichment.

We conclude that sensorimotor-enriched training constructs stronger associations between auditory L2 words and their L1 translations than commonly-practiced sensory-only methods in adults. Beneficial behavioral effects of gesture-enriched training are caused in part by responses within specialized sensory brain regions such as the bmSTS. The perception of spoken language may therefore rely not only on veridical auditory information stored in memory, but also on the sensorimotor context in which words are experienced. Several behavioral manipulations, including repetition, elaboration, and organization, have previously been shown to benefit memory retention. Our results call for the recognition of sensorimotor enrichment as a distinct behavioral memory aid characterized by the unique neural mechanism of sensorimotor simulation. The causal relation observed between sensory brain responses and enhanced behavioral outcomes advances the idea that pedagogical techniques based in learning by doing can be used as a strategy for enhancing memory and performance. Sensorimotor-enriched training methods are ripe for large-scale evaluation in classroom settings.

### Materials and Methods

**Participants**

Twenty-two right-handed native German speakers (15 females; \(M_{\text{age}} = 26.6 \text{ years, SD} = 4.7 \text{ years, range 18-35}\)) completed the study. The sample size was based on two previous experiments (\(n = 22\) per experiment) that estimated beneficial effects of gesture and picture enrichment on foreign language (L2) learning outcomes (Experiments 1 and 2).

None of the participants reported a history of neurological or psychiatric disorders, head injury, or any contraindications for transcranial magnetic stimulation (TMS). All participants reported normal hearing and normal or corrected-to-normal vision. None of the participants were raised in bilingual households. Of 32 total participants who registered for the study, 2 participants experienced adverse reactions to TMS and did not complete the initial testing sessions. Four participants were unable to return for additional testing sessions 5 months following the initial testing sessions, and 4 other participants were excluded due to poor localization of right or left bmSTS coordinates in individual participant space.

Written informed consent was obtained from all participants prior to the study. Participants were informed that the goal of the study was to test the effectiveness of different
vocabulary learning strategies in adulthood but they were naïve to the specific hypotheses. All participants were evaluated by a medical doctor prior to the study in order to be approved for TMS and magnetic resonance imaging (MRI). The study was approved by the ethics committee of the University of Leipzig.

**Stimuli**

Stimuli consisted of 90 pseudowords (Table S1). The pseudowords were derived from an artificial foreign language corpus referred to as ‘Vimmi’, developed by Macedonia and colleagues and intended for use in experiments on L2 learning. The corpus was created in order to control for participants’ prior knowledge of foreign languages and for differences between words (e.g., length, frequency) in natural languages. Vimmi words conform to rules of Italian phonotactics (words sound like Italian but do not exist in the Italian language). All Vimmi words used in the current study were composed of three syllables consisting of vowels and consonants.

The 90 Vimmi words and 90 German translations used in the current study were previously tested by Mayer and colleagues. Half of the 90 words were concrete nouns and the other half were abstract nouns. Lengths of concrete and abstract German words did not differ (concrete $M = 2.40$ syllables, $SD = 0.84$ syllables; abstract: $M = 2.69$ syllables, $SD = 0.90$ syllables). Frequency of the concrete and abstract words in written German did not differ (concrete frequency score: $M = 11.00$, $SD = 1.18$, range 9 to 13; abstract frequency score: $M = 10.96$, $SD = 0.98$, range: 9 to 13) (http://wortschatz.uni-leipzig.de/de).

**Videos, pictures, and audio files.** For each of the 90 Vimmi words, a 4 s color video was created using a Canon Legria HF S10 camcorder (Canon Inc., Tokyo, Japan). In each video, an actress performed a gesture that conveyed a word meaning. The actress was always positioned in the center of the video recording. She performed the gestures using head movements, movements of one or both arms or legs, fingers, or combinations of these body parts and maintained a neutral facial expression throughout each video. The word “bottle”, for example, was represented by the actress miming drinking from an imaginary bottle, and the word “good deed” was represented by the actress miming laying a donation in the imaginary hat of a homeless individual. The actress began and ended each gesture by standing motionless with her arms at her sides. Large gestures (e.g., steps or jumps) were restricted to a 1 m radius around the body's starting position. Gestures used to convey the meanings of abstract words were agreed upon by 3 independent parties.

A large black-and-white line drawing was created by a professional illustrator for each of
the 90 Vimmi words. Pictures conveyed word meanings by portraying humans, objects, or scenes. Pictures illustrating concrete nouns were mostly drawings of single objects, and pictures illustrating abstract nouns were often scenes. The complexity of the illustrations for concrete and abstract words was not matched, since similar differences are expected in natural teaching settings.

The same actress that carried out the gestures in the videos spoke the Vimmi and the German words in audio recordings. Words were recorded using a Rode NT55 microphone (Rode Microphones, Silverwater, Australia) in a sound-damped chamber. The actress is an Italian native speaker and recorded the Vimmi words with an Italian accent to highlight the foreign language aspect of the stimuli for German-speaking participants. Vimmi audio stimuli ranged from 654-850 ms in length ($M = 819.7 \text{ ms, } SD = 47.3 \text{ ms}$). For more details on the video, picture and audio files used in the current study, see Mayer and colleagues$^{22}$. Sample stimuli can be found at http://kriegstein.cbs.mpg.de/mayer_etal_stimuli/.

**Experimental Design**

The study utilized a $2 \times 2 \times 2 \times 2$ repeated-measures design. Within-participant independent factors were learning enrichment condition (gesture, picture), TMS condition (effective stimulation, sham stimulation), testing time point (5 days, 5 months), and $L2$ vocabulary type (concrete, abstract). Participants received both effective and sham TMS within the same session at each time point. Orders in which effective and sham TMS conditions were administered within each session was counterbalanced across participants within each time point and between time points.

**Procedure**

Participants learned $L2$ vocabulary over four consecutive days (days 1 to 4). The learning days were followed by two TMS sessions, which occurred on day 5 and month 5, shown in Fig. 1a. During the learning days, participants were trained on $L2$ words that were enriched with either gestures or pictures. During the TMS sessions, participants completed an $L2$ translation task while effective and sham TMS was delivered to the bilateral biological motion superior temporal sulcus (bmSTS). Structural brain scans used for TMS neuronavigation were obtained from all participants prior to the TMS sessions.

**$L2$ vocabulary learning.** Participants learned $L2$ words in two conditions. In the gesture learning condition, individuals viewed and performed gestures while $L2$ words were presented auditorily. In the control condition, individuals viewed pictures while $L2$ words were presented...
auditorily. Each day of learning comprised four 33-minute learning blocks. Blocks alternated between gesture and picture enrichment conditions. Each of the 45 Vimmi words included in a single learning block was repeated 4 times per block, yielding a total of 180 randomly-ordered trials per block. Participants took breaks of 10 minutes between blocks. During breaks, participants conversed with each other and consumed snacks and drinks that were provided. Enrichment condition orders were counterbalanced across participants and learning days.

Participants were instructed prior to the start of learning that the goal was to learn as many Vimmi words as possible over the 4 days of training. Participants received no further instruction during the training except to be informed about which learning condition would occur next (i.e., gesture or picture enrichment). Since the L2 vocabulary learning took place in groups of up to 4 individuals, training sessions occurred in a seminar room with a projector and a sound system. Audio recordings were played via speakers located on each side of the screen. The volume of the playback was adjusted so that all participants could comfortably hear the words.

The assignment of the 90 stimuli to learning enrichment conditions was counterbalanced such that half of the participants learned one set of 45 words in the gesture learning condition and the other set of 45 words in the picture learning condition. The other half of the participants received the reverse assignment of stimuli to gesture and picture conditions. This manipulation ensured that each Vimmi word was equally represented in both the gesture enrichment condition and the picture enrichment control condition.

In each gesture enrichment trial (Fig. 1b), participants first heard an L2 word accompanied by a video of an actress performing a gesture that conveyed the meaning of the word (shown for 4 s). They then heard the native language (L1) translation paired with a blank screen. Finally, the L2 word was presented a second time, again accompanied by the same video of the actress performing the gesture. Participants were asked to enact the gesture along with the actress during the second showing of each video. They were free to perform the gestures mirror-inverted or they could use their right arm when the actress in the video used her right arm, for example; they were asked to use only one of the two strategies throughout the learning period. In each picture enrichment trial (Fig. 1b), participants first heard an L2 word accompanied by a picture that conveyed the meaning of the word (shown for 4 s). They then heard the L1 translation paired with a blank screen. Finally, the same L2 word was presented a second time, again accompanied by the same picture. A motor task was not included in the picture enrichment condition as the enrichment of picture viewing with motor information (e.g., tracing an outline of presented pictures) has been shown to be less beneficial for learning than simply viewing the pictures without performing a motor task in adults. We therefore did not
combine picture enrichment with motor performance in the current study. Participants stood during all learning blocks. Standing locations during the training were counterbalanced over the 4 learning days.

On days 2, 3, and 4 of the L2 vocabulary learning, participants completed paper-and-pencil vocabulary tests prior to the training, shown in Fig. 1a. The vocabulary tests served to track each participant’s learning progress over the course of the experiment. Participants completed free recall, L1 translation, and L2 translation tests on each day. For further information on vocabulary tests, please see Mayer and colleagues\(^\text{22}\). The participant with the highest combined scores on the paper-and-pencil vocabulary tests across days 2, 3, and 4 was rewarded with an additional 21€ beyond the total study compensation of 211€. Participants were informed about the financial incentive on day 1 prior to the start of the learning blocks.

Prior to vocabulary learning on day 1, participants completed three psychological tests examining their concentration ability (Concentration test\(^\text{89}\)) \((M \text{ score } = 211.6, SD = 51.1)\), speech repetition ability (Nonword Repetition test\(^\text{90}\)) \((M \text{ score } = 98.2, SD = 8.8)\), and verbal working memory (Digit Span test\(^\text{91}\)) \((M \text{ score } = 18.7, SD = 3.7)\). Participants also completed a questionnaire on their prior knowledge of foreign languages and language learning experience.

**TMS translation task.** Participants performed a translation task (Fig. 1d) while undergoing effective and sham TMS in two TMS sessions (5 days and 5 months following the start of L2 vocabulary learning). The translation task consisted of four 6-minute blocks, each containing 45 words that had been presented on days 1 to 4. Each of the 90 words learned during on the learning days was presented twice during the TMS translation task, for a total of 180 test trials per TMS session. Effective and sham stimulation alternated across blocks, with half of the participants receiving effective stimulation during the first block and the other half receiving sham stimulation during the first block. Stimuli were ordered randomly within effective and sham stimulation blocks.

Each trial began with the written instruction “Press the button as soon as you know the translation” presented for 1.5 s on a screen. This was followed by the auditorily-presented L2 word accompanied by a black screen. A train of seven TMS pulses at 10 Hz delivered to the bilateral bmSTS began 50 ms after the onset of each word. Participants were asked to respond as soon as they recalled the L1 translation of the L2 word by pressing a button with their right index finger. If they did not know the L1 translation, they did not respond. Three seconds following L2 word onsets, a screen with four response options appeared and participants were given up to 2 s to select the correct L1 translation. The fourth response option was always “Unknown / Other word”; participants were told to select this option if they did not know the L1
translation or thought that the correct translation was different from the three options presented. They responded by pressing one of four buttons on the response pad with their index, middle, ring, or little fingers. Even if participants did not know the translation of the L2 word after hearing it, they were still able to select one of the four options presented. Responses were considered correct if participants pressed the correct button while the response screen was present. Participants were instructed to always respond as quickly and as accurately as possible. Each trial ended with a jittered inter-stimulus interval (0.5 to 1 s) paired with a black screen. Following the first TMS session, participants completed a questionnaire on strategies that they used to learn and remember the L2 words. Participants indicated that they recalled the L1 translation prior to the appearance of the four response options during fewer than half of all trials across the two TMS sessions ($M = 41.7\%$ of trials, $SE = 4.5\%$), leaving an insufficient number of trials for analysis of this task component. They selected a translation from the options presented during $M = 88.6\%$ ($SE = 3.6\%$) of trials across the two TMS sessions.

Several months following the first TMS session, participants were invited to participate in a second TMS session. The second session occurred approximately 18 weeks ($M = 18.0$ weeks, $SD = 1.4$ weeks) following the first session. Participants completed the same translation task as during the first TMS session while again undergoing effective and sham stimulation. Following the second TMS session, participants completed a questionnaire on strategies they used to remember meanings of the L2 words during the second session.

Finally, participants returned to complete the pencil-and-paper vocabulary tests 2 to 6 days ($M = 4.1$ days, $SD = 1.3$ days) after their second TMS session. Participants completed free recall, L1 translation, and L2 translation tests. Participants had no knowledge of the additional TMS and behavioral sessions until they were contacted a few weeks prior to their 5-month target testing dates. This was done in order to avoid potential rehearsal of the vocabulary during the 5-month interval between testing time points.

**Transcranial Magnetic Stimulation**

**Neuronavigation.** Stereotactic neuronavigated TMS was performed using Localite software (Localite GmbH, Sankt Augustin, Germany). Neuronavigation based on structural neuroimaging data from individual participants allows precise positioning of TMS coils $^{92,93}$. T1-weighted MRI scans for each participant were obtained with a 3-Tesla MAGNETOM Prisma-fit (Siemens Healthcare, Erlangen, Germany) using a magnetization-prepared rapid gradient echo (MPRAGE) sequence in a sagittal orientation (repetition time = 2300 ms, echo time = 2.98 ms, inversion time = 900 ms, flip angle = 9°, voxel size = 1x1x1 mm).
During each TMS session, participants were co-registered to their T1 scans. The two stimulation coils used in the current study were placed over Localite-indicated entry points of the respective target sites on the scalp. Entry points were those coordinates on each participant’s scalp that were the shortest distance to the target neural coordinates (right and left bmSTS). To stimulate the bmSTS bilaterally, a tangential coil orientation of 135° to the sagittal plane was applied with current flow within both stimulation coils reversed, resulting in a posterior to anterior (PA) current flow in the brain. A 135° coil orientation with a PA current flow is equivalent to a 45° coil orientation with an anterior to posterior (AP) current flow. The PA orientation has previously been used to disrupt cognitive functions94,95. Coils were secured in position using fixation arms (Manfrotto 244, Cassola, Italy).

Mean Montreal Neurological Institute (MNI) coordinates for bilateral bmSTS stimulation were derived from the functional MRI findings of Mayer and colleagues22: right bmSTS, x, y, z = 55, −41, 4; left bmSTS, x, y, z = −54, −41, −5. Mayer and colleagues22 found that participants translated auditorily-presented L2 words learned previously with gesture enrichment more accurately than L2 words learned without enrichment (auditory-only learning), referred to as a gesture enrichment benefit. Using multivariate pattern analysis (MVPA), they found that a classifier trained to discriminate BOLD responses to gesture-enriched and auditory-only words showed significant classification accuracy in the bmSTS. Classifier accuracy in the bmSTS positively correlated with the gesture enrichment benefit, suggesting a role of this area in improving learning outcomes following multisensory learning. In the current study, we stimulated the mean location across participants that demonstrated maximal classifier accuracy within the bmSTS. To ensure precise individual stimulation of target coordinates96,97, mean MNI coordinates for the two target sites (right and left bmSTS) were transferred into individual subject space using SPM8 (Wellcome Trust Center for Neuroimaging, University College London, UK, http://www.fil.ion.ucl.ac.uk/spm/).

**TMS parameters.** Two MagPro X100 stimulators (MagVenture A/S, Farum, Denmark) and a total of four focal figure-of-eight coils (C-B60; outer diameter = 7.5 cm) were used for stimulation. Signal software version 1.59 (Cambridge Electronic Design Limited, Cambridge, UK) was used to control the TMS pulse sequence. Presentation software (Neurobehavioral Systems Inc., Berkeley, CA, USA) was used for stimulus delivery, response recording, and to trigger TMS pulses.

An EIZO 19” LCD monitor approximately 1 m in front of the seated participant displayed task-related text (white letters, font: Arial, font size: 32 pt; black background). Shure SE215 sound isolating in-ear headphones (Shure Europe, Eppingen, Germany) were used to deliver L2
word recordings during the TMS sessions. Sound volume was individually adjusted prior to beginning the TMS task.

During each TMS session, a within-participants control condition was included by applying not only effective TMS to the bilateral bmSTS but also sham TMS. Sham TMS coils for each hemisphere were positioned at a 90° angle over each stimulation coil, as shown in Fig. 1c, and therefore did not effectively stimulate the brain. Coil locations were monitored and adjusted for head movements during the TMS sessions. The repetitive TMS protocol used (a seven-pulse train of 10 Hz TMS) was in line with published TMS safety guidelines.

Prior to the TMS translation task, each participant’s individual stimulation intensity was determined by measuring their resting motor threshold (RMT). To measure RMT, we stimulated the hand region of the left primary motor cortex (M1) using single-pulse TMS, resulting in the conduction of motor-evoked potentials (MEPs) in the relaxed first dorsal interosseous muscle (FDI) of the right hand. The RMT was defined as the lowest stimulation intensity producing 5 MEPs out of 10 consecutive TMS pulses that exceeded a 50 mV peak-to-trough amplitude. A meta-analysis by Mayka and colleagues provided mean stereotactic coordinates of the left M1 (x, y, z = −37, −21, 58 mm, MNI space), which were used to locate the M1 FDI hotspot. The coil used to elicit MEPs was oriented at 45° to the sagittal plane, inducing a PA current flow in the brain.

Effective and sham TMS intensity during the L2 translation task was set to 90% of each participant’s RMT. The same intensity was used for both TMS sessions for each participant (M = 40.1% of maximum stimulator output, SD = 5.6%).

Data Analysis

All participants who completed the study (n = 22) were included in the analyses.

To test our first hypothesis, we first ran a repeated measures two-way ANOVA with the factors learning condition (gesture, picture) and stimulation type (effective, sham) on translation response times. To evaluate whether the observed patterns of response times were due to speed-accuracy tradeoffs, we correlated response times in the multiple choice translation task were compared with accuracy (percent correct) for each learning condition, stimulation condition, and time point.

To test our second hypothesis on changes in L2 translation speed and accuracy over time, we computed change in translation speed and accuracy from day 5 to month 5 for the sham condition only. We then ran two-way repeated measures ANOVAs with factors learning condition (gesture, picture) and vocabulary type (concrete, abstract) on L2 translation speed and accuracy.
difference scores. Additionally, to explore how effects of bmSTS stimulation differed across testing time points, we ran a three-way repeated measures ANOVA on difference scores with factors learning condition (gesture, picture), stimulation type (effective, sham), and time point (day 5, month 5).

To test our third hypothesis regarding influences of vocabulary type on translation response times, we ran a four-way repeated measures ANOVA with factors learning condition (gesture, picture), stimulation type (effective, sham), testing time point (day 5, month 5), and vocabulary type (concrete, abstract). All pairwise comparisons were conducted using two-tailed Tukey HSD posthoc tests.
| German    | English    | Vimmi   | German    | English    | Vimmi   |
|-----------|------------|---------|-----------|------------|---------|
| Ampel     | traffic light | gelori  | Absage     | Cancellation | munopa |
| Anhänger  | trailer     | afugi   | Alternative | Alternative | mofibu |
| Balkon    | balcony     | usito   | Anforderung | requirement  | utike   |
| Ball      | ball        | miruwe  | Ankunft     | Arrival     | matilu  |
| Bett      | bed         | suneri  | Aufmerksamkeit | Attention  | fradonu |
| Bildschirm| monitor     | zelosi  | Aufwand     | Effort      | muladi  |
| Briefkasten| letter box | abota   | Aussicht    | View        | gaboki  |
| Decke     | ceiling     | siroba  | Befehl      | Command     | magosa  |
| Denkmal   | memorial    | frinupo | Besitz      | Property    | mesako  |
| Eintrittskarte| entrance ticket | edafe | Bestimmung | Destination | wefino  |
| Faden     | thread      | kanede  | Bitte       | Plea        | pokute  |
| Fahrrad   | bicycle     | sokitu  | Disziplin   | Discipline  | motila  |
| Fenster   | window      | uribo   | Empfehlung  | recommendation | giketa |
| Fernbedienung| remote control | wilbano | Gedanke     | Thought     | atesi   |
| Flasche   | bottle      | aroka   | Geduld      | Patience    | dotewa  |
| Flugzeug  | airplane    | wobeki  | Gleichgültigkeit | Indifference | frugazi |
| Gemälde   | painting    | bifalu  | Information | Information | sapezo  |
| Geschenk  | present     | zebalo  | Korrektur   | Correction  | fapoge  |
| Gitarre   | guitar      | masoti  | Langeweile  | Boredom     | elebo   |
| Handtasche| purse       | diwume  | Mentalität  | Mentality   | gasima  |
| Kabel     | cable       | zutike  | Methode     | Method      | efogi   |
| Kamera    | camera      | lamube  | Mut         | Bravery     | wirgonu |
| Kasse     | till        | asemo   | Partnerschaft | Partnership | nabita  |
| Katalog   | catalog     | gebamo  | Rücksicht   | consideration | ukowe |
| Kleidung  | clothes     | wiboda  | Sensation   | Sensation   | boruda  |
| Koffer    | suitcase    | mewima  | Stil        | Style       | lifawo  |
| Maschine  | machine     | nelosi  | Talent      | Talent      | puneri  |
| Maske     | mask        | epota   | Tatsache    | Fact        | botufe  |
| Papier    | paper       | serawo  | Teilnahme    | participation | pamagu  |
| Reifen    | tire        | wasute  | Tendenz     | Tendency    | peftia  |
| Ring      | ring        | guriwe  | Theorie     | Theory      | sigule  |
| Rucksack  | backpack    | lofisu  | Therapie    | Therapy     | giwupo  |
| Sammlung  | collection  | etuko   | Tradition   | Tradition   | uladi   |
| Schlüssel | key         | abiru   | Triumph     | Triumph     | gepesa  |
| Schublade | drawer      | lutepa  | Übung       | Exercise    | fremeda |
| Sonnenbrille| sunglasses  | woltume | Unschuld    | Innocence   | dafipo  |
| Spiegel   | mirror      | dubeki  | Veränderung | Change      | zalefa  |
| Straßenbahn| tram       | umuda   | Verständnis | Sympathy    | gorefu  |
| Tageszeitung| daily newspaper | gokasu  | Vorgehen    | Procedure   | denalu  |
| Telefon   | telephone   | esiwu   | Vorwand     | Excuse      | pirumo  |
| Teller    | plate       | buliwa  | Warnung     | Warning     | gubame  |
| Teppich   | carpet      | batewo  | Wohlstand   | Wealth      | bekoni  |
| Verband   | bandage     | magedu  | Wohltat     | Benefaction | migedu  |
Table 1 Vocabulary used in the experiment. 90 Vimmi and German words, and their English translations. Assignment of words to the gesture learning condition and the picture learning control condition was counterbalanced across participants, ensuring that each Vimmi word was represented equally in both learning conditions.

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