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The interplay between domain-general and domain-specific mechanisms during the time-course of verbal associative learning: An event-related potential study

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ABSTRACT

Humans continuously learn new information. Here, we examined the temporal brain dynamics of explicit verbal associative learning between unfamiliar items. In the first experiment, 25 adults learned object-pseudoword associations during a 5-day training program allowing us to track the N400 dynamics across learning blocks within and across days. Successful learning was accompanied by an initial frontal N400 that decreased in amplitude across blocks during the first day and shifted to parietal sites during the last training day. In Experiment 2, we replicated our findings with 38 new participants randomly assigned to a consistent learning or an inconsistent learning group. The N400 amplitude modulations that we found, both within and between learning sessions, are taken to reflect the emergence of novel lexical traces even when learning concerns items for which no semantic information is provided. The shift in N400 topography suggests that different N400 neural generators may contribute to specific word learning steps through a balance between domain-general and language-specific mechanisms.

1. Introduction

Humans present an exceptional ability to learn. In the case of language, this is evident when looking at the capacity to learn novel words. However, word learning is also a non-automatic, demanding task that requires motivation and active control (Abutalebi, 2008). Models of cognitive skill learning describe a gradual shift from highly controlled to more automatized processing during the acquisition of new knowledge or skills (Chein and Schneider, 2005; 2012). In line with this, the early stages of word learning are also known to require not only the coordinated engagement of specific language and memory systems but also domain-general regulatory functions such as attention, cognitive control, and motivation (Laine and Salmelin, 2010; Rodriguez-Fornells et al., 2009; Sliwinska et al., 2017). These domain-general mechanisms can regulate and monitor specialized cortical networks involved in word learning (Hagoort, 2019; Abutalebi et al., 2013). Thus, the subtle balance between domain-general and domain-specific neural resources might provide a highly flexible system involving both short- and long-term brain plasticity to acquire, integrate and automatically retrieve the learned information (Chein and Schneider, 2012; Jeon and Friederici, 2015). Here, we explored the neurophysiological signatures that underlie the shift between domain-general and domain-specific processing as it unfolds during verbal explicit associative learning. Of particular interest was the evolvement of the N400 component that has been strongly linked to associative word learning (Dittinger et al., 2016, 2017; Perfetti et al., 2005).

Psycholinguistic models propose that word learning may take place at different time scales, from the rapid learning of object-word associations to the slow build-up and consolidation of new episodic memory traces (Davis and Gaskell, 2009; McClelland et al., 1995; Sharon et al., 2011; Coutanche and Thompson-Schill, 2014). Sleep-related consolidation mechanisms are crucial for the binding of new words onto pre-existing lexical-semantic information (McClelland et al., 1995; Davis and Gaskell, 2009; Havas et al., 2018; Sestieri et al., 2017;

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Tamminen and Gaskell, 2013). Importantly, unlike proposals of classical memory models (Davis and Gaskell, 2009; McClelland et al., 1995), recent evidence suggests that rapid cortical encoding of new information could be independent of the medial temporal lobe (Hebscher et al., 2019; Brodt, 2018).

Capitalizing on its remarkable capacity to track the temporal brain dynamics of cognitive computations, event-related brain potentials (ERPs) have been extensively used to decipher word-learning mechanisms (McLaughlin et al., 2004; Dittinger et al., 2016; Mestres-Missé et al., 2007; Stein et al., 2006; Yum et al., 2014,; Morgan-Short, 2014). One of the most reliable findings observed in adults, children, and infants, is the modulation of the N400 component during the learning of new words (Friedrich and Friederici, 2004; 2017; Torkildsen et al., 2008; McLaughlin et al., 2004; Dittinger et al., 2016; Mestres-Missé et al., 2007; Stein et al., 2006; Elgort et al., 2015; Yum et al., 2014; Kuipers et al., 2017; Perfetti, 2007; Soskey, et al., 2016), a component associated with lexical and semantic processing (Kutas and Hillyard, 1980; Kutas and Federmeier, 2011). Previous studies have shown that the N400 is modulated when unknown words acquired meaning in both first (Perfetti, 2007; Mestres-Missé et al., 2007; Batterink and Neville, 2011) and second language learning (McLaughlin et al., 2004; Soskey et al., 2016; Dittinger et al., 2016; Stein et al., 2006), regardless of the learned language. However, results are mixed concerning the direction of the N400 modulations. While some studies have reported that learning is accompanied by a decrease in N400 mean amplitude (Stein et al., 2006; Bakker et al., 2015; Stuellein et al., 2016), others have shown an increase as a function of learning (McLaughlin et al., 2004; Yum et al., 2014; Dittinger et al., 2016, Soskey et al., 2016).

Importantly, previous studies have also shown different topographical distributions of N400, with some results showing canonical centro-parietal effects (Bakker et al., 2015; Soskey et al., 2016; Perfetti et al., 2005; Stein et al., 2006), while others showing more frontal or fronto-central effects (Bermúdez-Margaretto et al., 2018; Borovsky et al., 2010; Mestres-Missé et al., 2007; Yum et al., 2014). Concerning the latter findings, associative learning accompanied by N400 modulations over prefrontal regions has been taken to reflect the engagement of prefrontal cognitive control mechanisms for monitoring the initial build-up of episodic memory traces for novel words (Stein et al., 2006; Yum et al., 2014). Because newly created traces and associations are still weak, general cognitive control mechanisms may be needed support the maintenance of novel information in short-term memory during effortful retrieval (Rodriguez-Fornells et al., 2009). In contrast, at more advanced learning stages following the initial memory consolidation, processing of newly learned words might become more automatized, less susceptible to interference, and less dependent on cognitive control and monitoring processes during encoding and retrieval. In line with these ideas, several functional Magnetic Resonance Imaging (fMRI) studies have shown activations in cognitive control regions such as the prefrontal cortex, the inferior frontal gyrus, or the caudate during the initial stages of learning new words (Bradley et al., 2013; Mestres-Missé et al., 2008, 2009; Clements-Stephens et al., 2012; Ripollés et al., 2014; Raboyeau et al., 2010; Ferreira et al., 2015; Yang et al., 2015; Hosoda et al., 2013; Tagarelli et al., 2019 see also Rodriguez-Fornells et al., 2009 for a review). For instance, Bradley and colleagues (2013) showed increased activation in supplementary motor area, anterior cingulate and prefrontal cortex after only two hours of exposure to novel German vocabulary compared to native words. In the same line, Mestres-Misse and colleagues (2008, 2009, 2010) showed larger activations in the anterior cingulate cortex, left anterior inferior frontal and left middle frontal gyrus when trying to learn the meaning of novel words presented in meaningful compared to meaningless verbal contexts. Interestingly, larger activation in cognitive control regions such as the left middle temporal gyrus and the anterior cingulate cortex predicted word learning performance from verbal contexts (Mestres-Misse et al., 2010). In addition, recent longitudinal studies have examined the functional brain changes observed after long-term second language learning using fMRI (Barbeau et al., 2017; Grant et al., 2015; Liu et al., 2020). Barbeau and colleagues (2017) observed increased functional activation in the Inferior Parietal lobe (IPL) in English monolingual speakers after a 12-week intensive French language-training program. This result converges with previous studies on the importance of this region for second language acquisition, in relation to proficiency in bilingual speakers (Mechelli et al., 2004; Della Rosa et al., 2013; Abutalebi et al., 2015) and word learning (Lopez-Barroso et al., 2015; Mestres-Missé et al., 2008; Cornelissen et al., 2004; Golestani and Zatorre, 2004). Also relevant for the present study, Grant and colleagues (2015) observed in L2 learners who underwent six months of training an overall decrease in connectivity between cognitive control regions (medial and middle prefrontal cortex, anterior cingulate and inferior frontal gyrus) together with an increase in connectivity within semantic processing regions (e.g., between inferior frontal gyrus and middle temporal gyrus). This anterior (cognitive control) to posterior (semantic network) shift after training converges with previous results showing decreased connectivity between language and cognitive control areas after vocabulary learning (Ghazi et al., 2013; see also Liu et al., 2020).

Most of the studies focusing on the neural bases of word learning have used real familiar objects that were associated with unfamiliar L1 or L2 pseudowords or words (Stein et al., 2006; Bakker et al., 2015; Stuellein et al., 2016; McLaughlin et al., 2004; Yum et al., 2014; Dittinger et al., 2016, Soskey et al., 216). Only a few have explored the brain correlates of word learning in the most demanding situation where both the objects and pseudowords are unfamiliar (Laine and Salmelin, 2010; Hultén et al., 2009, 2010; Cornelissen et al., 2004). One could argue that learning new names for new objects may not represent word learning as semantic information is absent, but these studies indicate that verbal associative learning in such a situation is in fact both behaviourally and neurally similar to that of learning new names for familiar objects (Laine and Salmelin, 2010). At the behavioural level, participant reports during acquisition of new names for new objects have revealed a frequent use of self-generated semantic and phonological memory cues, e.g. by linking the new object to a familiar one that bears some similarity with it, or by associating the name of the object to a familiar name that phonologically resembles it (Grönholm et al., 2007). It is also worth noting that encounters with new names and new objects happen also in everyday life (consider e.g. seeing or hearing the word “dongle” together with the object for the first time), and such encounters lead to lexical acquisition even when knowledge of the object is either lacking or highly unspecific (e.g., “that gadget has something to do with computers”). Thus, learning to name novel objects can be taken as a particularly demanding form of associative learning, putting emphasis on cognitive control processes in word learning. We employed this paradigm to track the brain dynamics of verbal associative learning right from its start up to several months post learning. To our knowledge, a similar follow-up study with such a demanding learning paradigm has not been conducted before.

The present longitudinal study was designed to track the N400 modulations from the beginning of pseudoword-referent learning until the later stages of learning (after five days and four months post-training). Based on previous studies, we expected the new words to elicit a frontal N400 during day 1. We expected the N400 amplitude to decrease through learning blocks, reflecting the gradual build-up of associative memory traces. Moreover, as overnight consolidation should integrate the newly learned pseudowords into the mental lexicon (Havas et al., 2018; Dumay and Gaskell, 2012) that relies upon language-related cortical networks, we expected that improved recall performance through learning sessions would be accompanied with an N400 topography shift from frontal to parietal regions, reflecting an increase in retrieval automaticity. An important aspect of this study was that participants had to associate pseudowords to unknown objects, representing a particularly demanding form of associative learning. Therefore, ERP modulations observed in the present study cannot rely on the activation of pre-existing

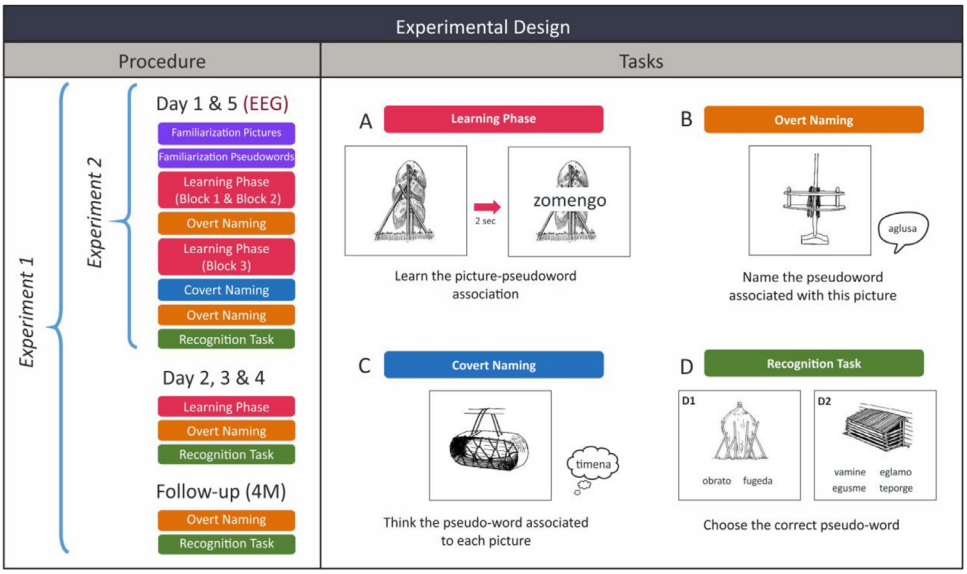


Fig. 1. Overview of the experimental design. In *Experiment 1*, participants performed a series of tasks (A-D) during a 5-day training program and a 4-month follow-up. *In Experiment 2*, the procedure was similar to Day 1 of Experiment 1. (A) Learning phase, (B) Overt-naming task, (C) covert-naming task, (D) two alternative-forced choice task (2-AFC). In *Experiment 2*, participants performed the same series of tasks from A to D. Note that a 4-AFC task was used in *Experiment 2*.

lexical memory traces (Angwin et al., 2014). Finally, we explored individual differences in cognitive control that may explain our behavioural and ERP data (Linck and Weiss, 2015; Kapa and Colombo, 2014).

In addition, we conducted a control experiment to rule out the confounding effects of stimulus repetition and increasing item familiarity on the N400 changes, as previous studies have suggested that the N400 amplitude may be modulated by these factors (Bermudez-Margaretto et al., 2018; Deacon et al., 2004). With this aim, we randomly assigned new participants to two groups differing in the consistency of the to-be-learned associations but being exposed to same number of repetitions. While participants of the consistent learning group (Cons) were presented with fixed object-pseudoword associations, participants of the inconsistent learning group (Icons) were presented with random pseudoword-referent pairings that render learning impossible. If the N400 amplitude decrease observed in Experiment 1 reflects stimulus repetition/familiarity, we expected to observe a similar decrease in N400 amplitude in both groups. In contrast, if the N400 modulations rather reflect the gradual buildup of memory traces for object-pseudoword pairs, we expected to see a decrease in N400 amplitude in the Cons group only.

2. Materials and methods

2.1. Participants

Twenty-five healthy volunteers (13 females, mean age: 22 ± 3.19) participated in *Experiment 1*. They were all right-handed and had a normal or corrected-to-normal vision, and reported no history of neurological deficits. All participants were Spanish-Catalan bilinguals except for two Spanish monolinguals. For the follow-up evaluation, five participants dropped out of the study (N=20).

For *Experiment 2*, a total of 38 healthy volunteers were recruited with 19 participants randomly assigned to the learning group (Cons, 10 females, age: 23 ± 3.32) and the other 19 participants to the no learning group (Icons, 9 females, age: 23 ± 2.49). They were all right-handed, had a normal or corrected-to-normal vision, and reported no history of neurological deficits. All participants were Spanish-Catalan bilinguals.

For both experiments, participants were informed about the study procedure, gave their written consent, and were paid 60€ for their participation in the 5-day training sessions and 10€ for the follow-up evaluation. The study was approved by the local ethics committee.

2.2. Stimuli

A set of 139 unfamiliar black-and-white objects representing farming artifacts were selected from the Ancient Farming Equipment (AFE) word-learning paradigm (Laine and Salmelin, 2010). Familiarity scores for these 139 unfamiliar objects (0-5 from totally unfamiliar to very familiar) were obtained from 20 additional students from the University of Barcelona (Mean: 2.58; SD: 0.61). Based on these ratings, the 120 most unfamiliar objects were selected.

A set of 120 tri-syllabic pseudowords was created using the B-Pal software (Davis and Perea, 2005). The pseudowords respected the phonotactic rules of Spanish, representing six different Consonant-Vowel (CV) structures (CVCVCV, VCVCVC, VCVCV, VCCVCV, CVCVCCV, and VCVCCV) and were always visually presented.

2.3. Procedure and tasks

2.3.1. Experiment 1

Experiment 1 included five consecutive daily training sessions and a follow-up evaluation four months later (see Fig. 1). During the first and last days of the training program, the participants first performed a pre-exposure task during which they were exposed to novel objects and pseudowords, a learning phase with an overt-naming task in-between the learning. Consecutively, the participants performed a covert-naming task, an overt-naming task, and a 2-alternative forced-choice pseudoword-object matching task (2-AFC; see below for detailed task description). During the second, third, and fourth training days, the participants performed the learning and the 2-AFC task. In the 4-month follow-up assessment, the participants performed the overt-naming and the 2-AFC task. EEG was recorded during Day 1 and Day 5.

On the first day, before starting the training sessions, we administered a Language history questionnaire (Bilingualism and Language switching, Rodriguez-Fornells et al., 2012) and two tasks associated with cognitive control and working memory [the semantic and phonological fluency tasks (category of animals and words beginning with the letter "p") and an auditory working memory task (WAIS-III's Digit Span, mean score of forward and backward span). Verbal fluency was chosen because of its previous association with both aspects, effortful word retrieval and cognitive control (Hughes and Bryan, 2002; Carpenter et al., 2020). More importantly, verbal fluency has been consistently associated with the amplitude of the N400 component during lexical retrieval (Federmeier et al., 2002, 2010). Digit span was chosen as a measure of working memory and cognitive flexibility, which has previously related

to word learning (Baddeley et al., 1998). After this brief examination, participants underwent the training sessions.

First, participants performed a pre-exposure phase. During this phase, the 120 novel objects were randomly presented for 2 seconds each. Additionally, five objects from the AFE paradigm (objects with the highest familiarity scores in the initial item selection) were randomly presented and participants were asked to press a response button when the target objects appeared. This was done to maintain a constant level of attention throughout the pre-exposure phase. Importantly, although not reported here, the familiarization task was included to explore the brain responses to novel items (pseudowords and pictures) when the participants have been instructed to just pay attention to the stimuli or learn them. Besides, we wanted to avoid pure novelty ERP effects during the learning phase (presenting novel pictures for first time) as the effects of novelty on brain activation have been systematically reported in previous studies (Tulving et al., 1996; Duzel et al., 2003; Lisman and Grace, 2005; Wittmann et al., 2008). In this sense, pre-exposure to the new items without learning instructions allowed participants to familiarize with the new object-like configurations and avoiding other contamination from novelty effects in the ERPs gathered during learning. Nonetheless, in the present work we decided to focus on the learning phase only. A similar pre-exposure phase was also performed for the pseudowords. In this case, the 120 novel words were randomly presented for 2 seconds each. Besides, five real words were randomly presented and participants were asked to press a response button when a real word appeared. The results of this task are not presented in the present work.

In the learning phase, the 120 object-pseudoword pairs were randomly presented within each block. The participants were required to pay attention to the object-pseudoword associations and encouraged to learn as many as they could. In each learning trial, a novel object was presented on the screen for 2 seconds, and the associated pseudoword appeared above it for 1 second. The first part of the learning phase consisted of 480 trials divided into 4 blocks, while the second part (after the overt naming task) consisted of 240 trials divided into 2 blocks. During the learning phase, a short break was taken every 30 trials to avoid fatigue. The overt-naming task was done shortly before the end of the learning task to boost learning, as overt naming has been shown to facilitate lexical access and word learning (Strijkers et al., 2011).

The level of learning was assessed using two different tasks with no feedback between trials at two different time points.

Overt-naming task: The first assessment of learning was made with the Overt-naming task that allowed to behaviourally assess the ability to actively use the recently learned pseudowords. Moreover, overt-naming tasks rely on active retrieval processes (Costa et al., 2009; Laine and Martin, 2006), which in turn, are known to boost learning (Agarwal et al., 2012; Pyc and Rawson, 2009; Roediger and Butler, 2011). During this task, each of the 120 objects was presented on the screen for 3 seconds, while the participants had to overtly name the pseudoword associated with the object. Importantly, no feedback was provided between trials. To control for possible order effects, eight randomized sequences of the objects were created, and the presentation of these sequences was counterbalanced across days and participants. Participants' responses were digitally recorded for subsequent scoring. We considered the response as correct when the participant named the object without any without syllable or phoneme error. Because the pseudowords respected the phonotactic rules of Spanish, participants made no mispronunciations. However, a missing syllable or phoneme was considered as incorrect. The EEG data obtained in this task are not reported here.

Covert-naming task: This task was performed before the last naming task to induce active retrieval processes known to facilitate learning and to gather EEG activity to pseudowords without the muscular artefacts induced by overt-naming (Strijkers et al., 2011). During this task, each of the 120 objects was presented on the screen for 3 seconds, while the participants were asked to think about the pseudoword without overtly naming it. To maintain the level of attention constant during the task, a red square appeared around the object in 10% of the trials, prompting the participants to name that object overtly. For this task, 5 randomized versions were created (one version for each time that the task was administered) and counterbalanced across sessions and participants.

2-AFC task: The second assessment of learning was made with the 2-AFC task. During this task, each of the 120 objects was presented on the screen for 2 seconds, together with two possible pseudowords appearing below, and followed by a question mark for 500 ms prompting the participants to respond. The participants had to choose which of the two pseudowords was the one associated with the object by pressing the right or the left mouse button. One of the two pseudowords was the correct choice, and the other one had been presented during the learning phase but had never been associated with that object. No feedback was provided. Two randomized sequences were created and counterbalanced across sessions and participants.

In the 4-month follow-up evaluation, the participants came back to the laboratory to perform a new randomized version of the overt-naming and 2-AFC task only. Importantly, participants were contacted shortly in advance but were not aware of the purpose of the follow-up and were not exposed to the experimental materials (pseudowords and objects). Therefore, the participants were instructed to do their best in remembering and recalling the object-pseudoword associations. Due to practical reasons, we could not grant access to the same experimental room and EEG data could not be collected during this follow-up.

2.3.2. Experiment 2

A few days before coming to the laboratory, six objects from the AFE paradigm were sent by email and the participants were asked to memorize them. At the beginning of the experimental session, we first confirmed sufficient familiarization by asking the participants to recognize the six objects presented by pair together with fourteen extra objects not used in the experiment. During the learning phase, the six objects (catch trials) appeared twice in each block and were pseudo-randomly presented with a minimum of two learning trials in-between. The catch trials allowed maintaining the level of attention constant throughout the learning phase. In the learning phase, the Cons group was exposed to fully consistent object-pseudoword associations as in *Experiment 1*. By contrast, the Icons group was presented with fully inconsistent associations so that none of the 120 words was presented more than once with the same object (see Fig. 1). Therefore, no learning was possible. This control group was important to rule out the effect of repetition and novelty on the N400 modulations as shown in previous studies (Bermudez-Margaretto et al., 2018; Deacon et al., 2004). Both groups were instructed to learn as many associations as they could. Nonetheless, as opposed to the learning phase of *Experiment 1*, the participants had also to press a response button for the catch trials which corresponded to the 6 familiarized objects. The duration of the trials and the block structure were the same as in *Experiment 1* for both groups.

For the AFC task, we used a four-alternative pseudoword-object matching task (4-AFC) instead of 2-AFC to avoid the ceiling effect obtained in *Experiment 1*. The 120 objects were randomly presented for 3 seconds together with 4 possible pseudowords below, followed by a question mark for 500 ms prompting the participants to respond. The participants were asked to press buttons 1 to 4 to indicate which word was associated with the new object. For the Cons group, only one of the pseudowords was correct, while the 3 other pseudowords were presented during learning but never with that specific object. For the Icons group, one of the six pseudowords had been associated with the object during the learning task, and the other three pseudowords had never been associated with that object. The correct pseudoword in the Icons group was counterbalanced across blocks and tasks so that all pseudowords were presented the same number of times.

The pre-exposure, overt-naming, and covert-naming tasks were identical to the ones in *Experiment 1*. The EEG was recorded during the entire experiment. The pre-exposure task was maintained in such a way that

the number of pictures and word repetitions was the same as in *Experiment 1*.

2.3.3. EEG data acquisition and analyses

The EEG signal was recorded from the scalp (0.01 Hz high-pass filter with a notch filter at 50 Hz; Sampling rate 250Hz) using tin electrodes mounted in an electrocap (Electro-Cap International) and located in 29 standard positions (International 10/20 system sites: Fp1/2, F3/4, C3/4, P3/4, O1/2, F7/8, T3/4, T5/6, Fz, Cz, Pz, Fc1/2, Fc5/6, Cp1/2, Cp5/6, Po1/2) using a BrainAmp amplifier (BrainVision acquisition software, Brain Products©) during the entire experimental session of Day 1 and Day 5 in *Experiment 1* and during the entire session in *Experiment 2*. An electrode placed at the lateral outer canthus of the right eye served as an online reference. The ground electrode was located on the scalp at FCz position. Biosignals were re-referenced off-line to mean activity at the two mastoidal electrodes. Vertical eye movements were monitored with an electrode placed at the infraorbital ridge of the right eye. Electrode impedances were kept below 5 kΩ. Electrophysiological data were analyzed using ERPLAB 13.5.4b. The EEG was filtered off-line using a 30 Hz low-pass filter only for display figures and no off-line high-pass filter was applied. Epoch rejection criteria were individually determined using a simple voltage threshold within a range of +/- 75 μV for eye electrode and +/- 50 μV for the other channels and forward visually checked for each trial and participant. Importantly, the EEG data analyzed and reported in the present manuscript were collected during the learning phase described above. Specifically, epochs of 900 ms were time-locked to pseudoword presentation considering a -100 ms pre-stimulus time-window used for baseline correction.

2.3.4. Behavioural data analysis

For *Experiment 1*, we analyzed separately for each task (overt-naming and 2-AFC task) the percentage of correct responses (CR) using repeated-measures ANOVA with Day (Day 1, 2, 3, 4, 5 and 4-months follow-up) as a within-subject factor. The Greenhouse-Geisser correction was applied when necessary. Furthermore, as a measure of pseudoword forgetting, we computed the words retrieved on Day 5 minus the words retrieved in the 4-month follow-up evaluation divided by the number of words retrieved on Day 5 (Day5 - Follow-up / Day5). This index was used to explore the relationship between the participant's ability to learn the words and neuropsychological factors. Only 20 participants were included due to the drop of 5 participants in the follow-up evaluation.

For *Experiment 2*, we analyzed separately for each task (overt-naming and 4AFC task) the percentage of correct responses using independent-samples *t*-tests. We also used one-sample *t*-tests for each group to determine whether participants' performance was significantly above chance level. For the Icons group, we considered a correct answer in the overt-naming task when a participant named at least one of the six different pseudowords presented during the learning blocks. All the analyses were performed with IBM SPSS statistics 23 (SPSS, Chicago, Illinois).

2.3.5. ERP analyses

For both experiments, we analyzed the ERPs time-locked to the pseudowords presented during the different blocks of the learning phase. To explore the evolution of these ERPs through learning, the four blocks of the first part of the learning task were averaged in two blocks (Block 1 and Block 2), and the two blocks of the second part (after the overt naming) were averaged in one block (Block 3, see Fig. 1). In *Experiment 1*, based on visual inspection of the waveforms as well as on previous literature (Soskey et al., 2016; see Kutas and Federmeier, 2011 for a review), we analyzed the N400 elicited by pseudowords in the 350-550 ms time-window. Specifically, we extracted the mean ERP amplitude to pseudowords in the 350-550 ms time-window for each electrode, participant and learning block, as done in previous studies on word learning (Dittinger et al., 2016, 2019). For each participant, only correctly learned pseudowords (correct items in the 2-AFC task of Day 5) were included in the analyses. The criterion for classifying a word correctly learned was based on the individual correct responses obtained in the 2-AFC task of the last training day (correct items in the 2-AFC task of Day 5). This criterion allowed us comparing ERPs to the same items within each individual on both days (albeit being different items for different individuals). We performed repeated-measures ANOVA on nine channels (F3, C3, P3, Fz, Cz, Pz, F4, C4, and P4) with four factors: Day (Day 1, Day 5), Block (Block 1, Block 2, Block 3), Lateralization (Left, Central, and right) and Antero-posterior (Frontal, Central, and Parietal). In *Experiment 1*, Block 1, 2, and 3 of Day 1 included an average of 149 [range: 69-223], 147 [range: 50-219], and 149 trials, respectively [range: 77-223]. Block 1, 2, and 3 of day 5 included an average of 150 [range: 88-218], 148 [range: 72-226] and 152 trials, respectively [range: 98-227]. In *Experiment 2*, the Consistent group had an average of 199 [range: 158-228], 181 [range: 94-310] and 192 trials per Block [range: 123-231]. The Inconsistent group had an average of 189 [range: 71-228], 196 [range: 133-234] and 197 trials per Block [range: 144-233].

We investigated possible associations between the main ERP effects and behavioural performance, as well as cognitive control individual differences (verbal fluency and working memory). For the ERP effects used in these correlations, we extracted the mean N400 amplitude of the within- (Block 1 minus Block 3 of Day 1) and between-session effect (Block 1 minus average of Day 5) over two regions of interest where the topographical distribution showed larger effects. Specifically, we used the mean amplitude between 350 and 550 ms averaged across Pz, P4 and Cp2 for the within-session effect (see Fig. 4A), and across Fz, Fcz, Cz, Fc1 and Fc2 for the between-session effect (see Fig. 4B). Pearson correlation was used for the analysis, and False Discovery Rate (FDR) correction was applied for each neuropsychological test and each behavioural measure.

Finally, we computed current source density (CSD) maps to localize the patterns of the N400 current flows using the CSD toolbox (Kayser and Tenke, 2006) in Matlab. This approach, is largely recognized as a reference-free method allowing the sharpening of ERP topographies in a physiologically meaningful manner (Nunez and Westdorp, 1994). The CSD transformation allows establishing a more reliable link between the electrophysiological activity and the underlying cognitive processes by enhancing local activity and suppressing activity with broader spatial extent (Vidal et al., 2015; Kayser and Tenke, 2015; Vilà-Balló et al., 2017; Perrin et al., 1987; Weiss et al., 2016).

In Experiment 2, we computed the mean N400 amplitude to pseudowords in the 350-550 ms time-window for each electrode, participant and learning block, as done in Experiment 1. However, we included all the trials in the analysis due to the mixed-model design. An ANOVA was used with Group (Cons vs. Icons) as between-subject factor and Block (Block 1, Block 2, and Block 3), Lateralization (Left, Central, and Right) and Antero-posterior (Frontal, Central, and Parietal) as within-subject factors including the same electrodes as in *Experiment 1*.

For the Cons group only, we analyzed ERP differences in mean N400 amplitude between learned and non-learned words by averaging the ERPs throughout blocks and by performing a repeated-measures ANOVA with the factors Item (learned words and non-learned words), Lateralization (Left, Central, and Right) and Antero-posterior (Frontal, Central, and Parietal). For each ANOVA, Greenhouse-Geisser sphericity corrections were applied when appropriate. Post-hoc tests were conducted using pairwise *t*-tests corrected for multiple comparisons using the Benjamini-Hochberg FDR procedure (Benjamini and Hochberg, 1995).

3. Results

3.1. Experiment 1

3.1.1. Behavioural data

For *Experiment 1,* we analyzed separately the overt-naming and 2-AFC task. For the overt naming we computed the percentage of correct responses (CR) using repeated-measures ANOVA with Day (Day 1, 2, 3, 4, 5 and 4-months follow-up) as a within-subject factor (Fig. 2). Results showed that the participants increased their number of CR over the 5

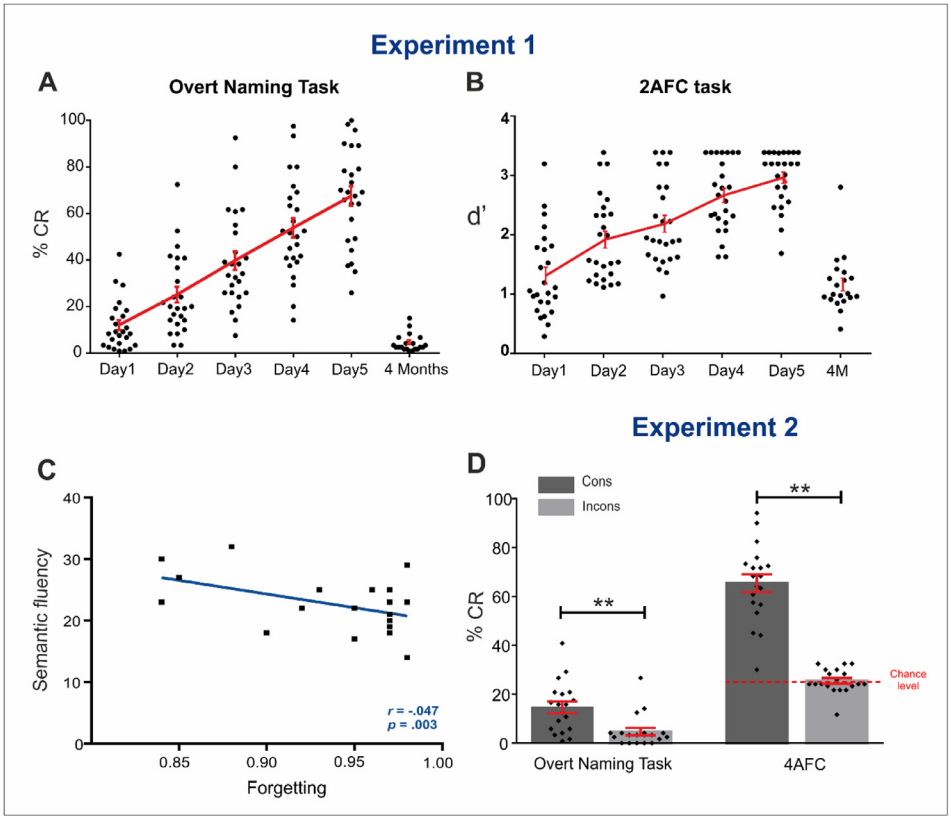


Fig. 2. Behavioural data. *Experiment 1*: (A) Percentage of correct responses in the overt-naming task across sessions; (B) d' in the 2-AFC task across sessions; (C) The negative correlation between the score in semantic fluency and 4-month forgetting. (D) *Experiment 2*: Percentage of correct responses in both the overt-naming task and the 4-AFC task for the consistent learning (Cons) and the inconsistent learning group (Icons). Dots and diamonds represent individual values and bars correspond to the mean and standard error of the mean (SEM). Notice that in section C, only 20 participants were included in the correlation due to the drop off of 5 participants in the follow-up evaluation.

days of training in both tasks: the overt-naming task [main effect of Day: $F(5, 95) = 145.89$; $p < .0001$]. For the 2-ACF task, we computed the d' and performed the same repeated measures ANOVA as for the overt naming. As shown on Fig. 2B, we observed a clear increase in word recognition throughout the training days [main effect of Day: $F(5, 95) = 77.6$; $p < .0001$].

Remarkably, although all participants were able to learn along with the training sessions, the number of pseudowords that participants were able to retrieve in the follow-up evaluation was quite low (forgetting: mean = .93, SEM = .01, Fig. 2A). Nonetheless, the average rate of correctly recognized words in the 2-AFC task was quite high (mean = 77.66, SEM = 1.76; Fig 2B), which suggests that considerable information was retained. Interestingly, we found a significant correlation between the forgetting index and semantic fluency performance ($r = -0.47$; $p = .03$), so that a better performance in semantic fluency was associated with less forgetting in the follow-up evaluation (Fig. 2C). No other significant correlations with the other neuropsychological tests (phonological fluency or working memory) were found (see Supplementary Table 1).

Table 1
Results from the repeated measures ANOVA of *Experiment 1* for the mean N400 (350-550 ms) with 4 factors: Day (Day 1, Day 5), Block (Block 1, Block 2, Block 3), Lateralization (Left, Central, and right) and Antero-posterior (Frontal, Central, and Parietal). Only main effects of the experimental manipulations and interactions with electrode factors are reported here, thus, no main effects of electrode factors (Lateralization and Anteroposterior) are shown. *Lat = Lateralization. Anteropost = Anteroposterior.

Repeated measures ANOVA *Experiment 1*			
Day	**$F = 9.89$**	Day x Anteropost	**$F = 13.62$**
(1, 24)	**$p = .004$**	(2, 48)	**$p = .001$**
Block	**$F = 14.39$**	Block x Anteropost	$F = 2.11$
(2, 48)	**$p < .001$**	(4, 96)	$p = .117$
Day x Block	**$F = 14.49$**	Day x Block x Lat	**$F = 5.92$**
(2, 48)	**$p < .001$**	(4, 96)	**$p = .001$**
Day x Lat	$F = 2.10$	Day x Block x Anteropost	**$F = 4.78$**
(2, 48)	$p = .145$	(4, 96)	**$p = .013$**
Block x Lat	**$F = 3.39$**	Day x Block x Lat x	$F = .78$
(4, 98)	**$p = .023$**	Anteropost	$p = .577$
		(8, 192)	

3.1.2. ERP results

Results of the repeated measures ANOVA with the factors Day (Day 1, Day 5), Block (Block 1, Block 2, Block 3), Lateralization (Left, Central, and right) and Antero-posterior (Frontal, Central, and Parietal) are shown in Table 1. A frontally distributed N400 was elicited by the presentation of new words during the first block of Day 1 (see Fig. 3). This frontal N400 was modulated by learning with a decrease of amplitude in Block 2 and 3, as evidenced by a main effect of Block [$F(2,48) = 14.39$; $p < .001$] and a significant Day x Block interaction [$F(2, 48) = 14.49$; $p < .001$]. The decrease in N400 amplitude across blocks was significant in Day 1 [Day 1: Block 1 vs Block 2 ($t(24) = -3.05$; $p = .006$); Block 2 vs Block 3 ($t(24) = -4.15$; $p < .001$)] but not in Day 5 during which it reached a plateau [Day 5: Block 1 vs Block 2 ($t(24) = 1.89$; $p = .07$); Block 2 vs Block 3 ($t(24) = -1.56$; $p = .132$)]. This was further evidenced by separated analyses by day showing a significant effect of Block during Day 1 only [Day 1: main effect of Block $F(2, 48) = 23.17$; $p < .001$; Day 5: main effect of Block: $F(2, 48) = 2.15$; $p = .13$].

Importantly, the scalp distribution of the N400 during the first block was frontocentral (see Fig. 4A, Block 1 Day 1 topography in the right panel) and showed a shift in the distribution along with the experiment. The within-session N400 effect (i.e., difference waveform of block 1 minus block 3 of Day 1) showed a centro-parietal distribution that was clearly visible on the CSD maps (Fig. 4A). This high spatially resolved analysis allowed to show the N400 sources in red (i.e. the current flow from the brain towards the scalp) and sinks in blue (the current flow from the scalp into the brain; see Nunez and Srinivasan, 2006). Here, the mean N400 within-session effect relied on the involvement of a strong right lateralized parietal sink and a weaker frontal sink. In contrast, the between-session N400 effect (difference waveform of Block 1 of Day

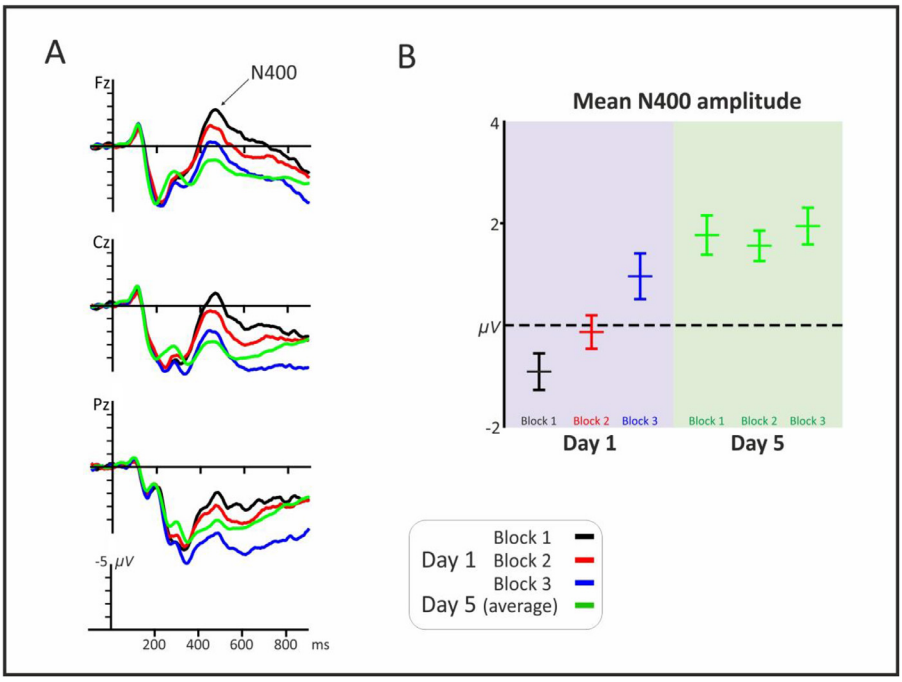


Fig. 3. A) ERP grand averages to pseudowords at midline electrodes across 25 participants during each learning block (black = block 1 of Day 1, red = block 2 of Day 1, blue = block 3 of Day 1, green = average of the three blocks of Day 5). B) Time-course of within- and between-sessions mean N400 amplitude for all the learning blocks of Day 1 and Day 5 in the 350-550 ms time-window averaged over F3, Fz, and F4 electrodes.

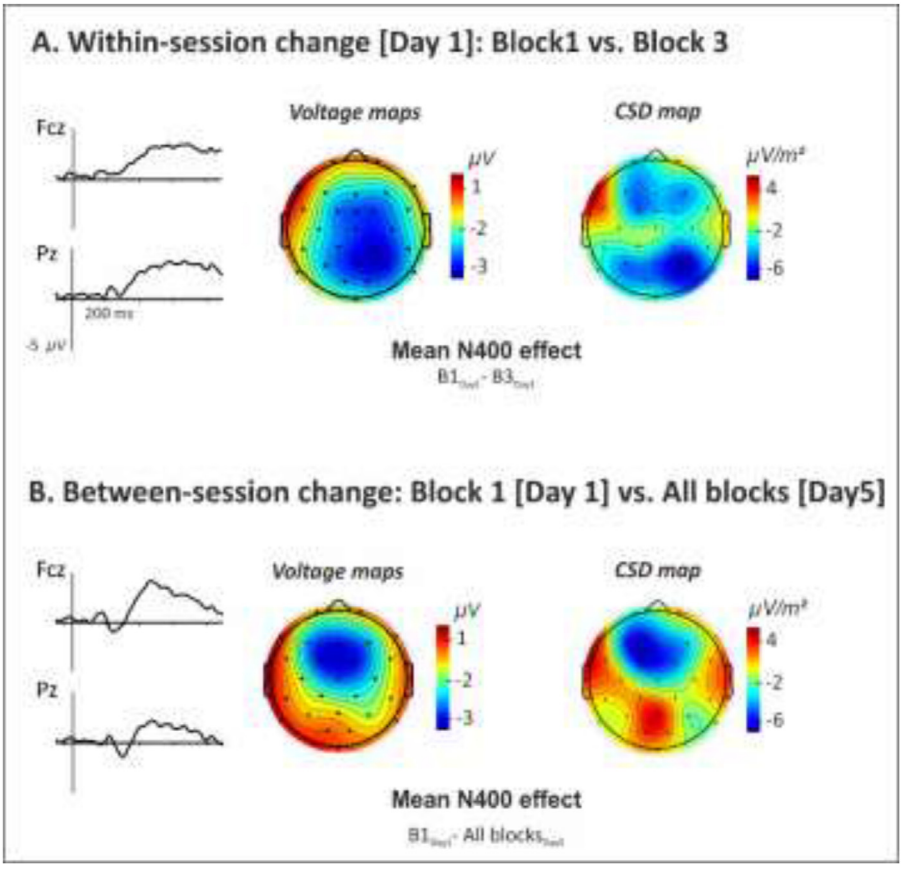


Fig. 4. Difference waveform, voltage and current source density maps (CSD) of the within- and between-sessions changes. A) Distribution of the difference waveform of the within-session effect (Block 1 - Block 3 of Day 1). B) Distribution of the difference waveforms between-sessions effect (Block 1 [Day 1] - All blocks [Day 5]). For each sub-figure the difference waveform at Fcz and Pz electrodes is shown on the left. The voltage and CSD maps of the difference waveforms are shown on the right (350-550 ms time-window mean amplitude). Notice the waveform change from a central-parietal N400 within-session effect (A) to a more frontally distributed N400 between-sessions effect (B). The CSD maps are shown on the right. Notice the sharp contrast between the voltage and the CSD maps that show the clear involvement of parietal and frontal sources for within and between-sessions N400 effects respectively.

1 minus the average of Day 5) showed a very clear medial frontal topography [Day x Block x Antero-posterior interaction: $F(4,96) = 4.78$; $p = .013$; see Table 1 and Fig. 4B, voltage maps and CSD panels]. Importantly, the sink and sources underlying the N400 between sessions effect were different from those of the within-session effect and showed a more focal frontal sink.

Regarding the relationship between individual differences and ERP effects, we observed a significant negative association between the mean N400 between-sessions effect (difference Block 1 of Day 1 - the average of all Blocks of Day 5) and the scores in the letter fluency task ($r = -.45$; $p = .025$, Fig. 5), so that participants with higher phonemic fluency performance showed greater changes in the N400 between day 1 and

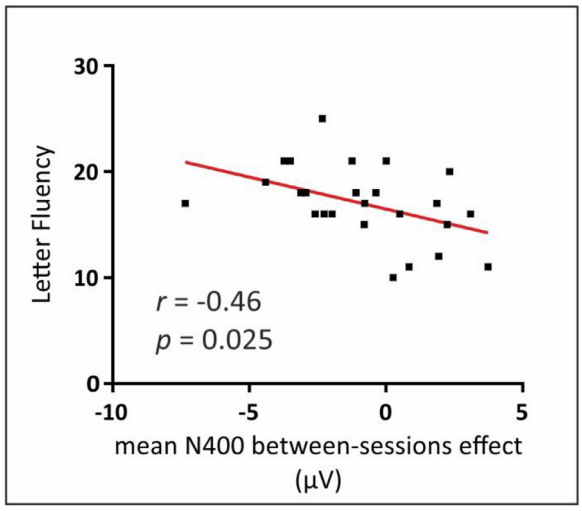


Fig. 5. Scatter plot showing the correlation between the mean N400 between-sessions effect (Block 1 of Day 1 minus average of Day 5) in the 350-550 ms time window averaged over 5 fronto-central electrodes (Fz, Cz, Fcz, Fc1, Fc2) and participant's level of performance in the verbal fluency letter task.

day 5 (frontal distribution). No significant correlations were found between the other cognitive tasks or learning performance with the within-session N400 effect (parietal distribution, see Supplementary Table 2).

3.2. Experiment 2

3.2.1. Behavioural data

For Experiment 2, the Cons outperformed the Icons group in both tasks (4-AFC task: Cons: 65.44% CR, SD = 15.7; Icons: 25.48% CR, SD = 5.04; overt-naming task: Cons: 14.65%, SD = 10.44; Icons: 4.74%, SD = 6.54; see Fig. 2D) as evidenced by significant group differences in the overt-naming [$t(36) = 3.51$; $p = .001$] and in the 4-AFC task [$t(36) = 10.52$; $p < .001$]. These results were confirmed by further pairwise *t*-tests showing significant group differences in both the overt-naming [$t(36) = 4.93$; $p = .001$] and the 4-AFC task [$t(36) = 11.93$; $p < .001$]. Importantly, in the 4-AFC, the Cons group (M = 65.44, SD = 15.76) performed significantly above chance level (25% of correct responses; $t(18) = 11.18$; $p < .001$) which was not the case for the Icons group (M = 25.48, SD = 5.04; $t(18) = .42$; $p < .681$), indicating that the latter group was not able to associate the words to the objects.

3.2.2. ERP results

Here, we aimed to replicate the results of Experiment 1 and to rule out the effect of repetition on the N400 modulations as shown in previous studies (Bermudez-Margaretto et al., 2018; Deacon et al., 2004). In addition to a new learning group, we introduced a control group in which participants were presented with fully inconsistent pseudoword-object associations where new words could not be systematically associated with any referent. Results of the repeated-measures ANOVA with the factors group (Cons, and Icons), Block (Block 1, 2, 3), Lateralization (Left, Central, and Right), and Antero-posterior (Frontal, Central, and Parietal) are shown in Table 2. We observed different learning dynamics between the two groups at the level of the N400 [Group x Block interaction: $F(2,72) = 3.98$; $p = .02$]. Separate analyses in the Cons group showed differences across blocks [Block x Antero-posterior interaction: $F(4,72) = 6.28$; $p = .002$], thus confirming the results obtained in *Experiment 1*. New pseudowords elicited a frontal N400 in Block 1 that decreased in Block 2 and 3 (Fig. 6A), with a significant decrease in Block 3 ($t(18) = -3.88$; $p = .002$, corrected for multiple comparisons). As found in *Experiment 1*, the within-session N400 effect was centro-parietal in both the voltage and CSD maps (Fig. 6C). In the Icons group, the main effect of Block was significant [$F(2,36) = 3.95$; $p = .03$], but pairwise *t*-tests failed to reach significance after correction for multiple comparisons (see Fig. 6A and Table 3 and 4).

We further investigated the functional role of the N400 in the build-up of new semantic associations in the Cons group by comparing ERPs to correctly learned and non-learned words averaged across blocks. Results of the ANOVA with the factors Item (Correct, Incorrect), Lateralization (Left, Central, and Right), and Antero-posterior (Frontal, Central, and Parietal) revealed that non-learned words elicited a larger mean N400 than learned words between 350 and 550 ms [main effect of Item:

Table 2
Results from the mixed model ANOVA of *Experiment 2* for the mean N400 (350-550 ms) with Group (Cons vs. Icons) as between-subject factor, Block (Block 1, Block 2, and Block 3), Lateralization (Left, Central, and Right) and Antero-posterior (Frontal, Central, and Parietal) as within-subject factors. Only main effects of the experiment manipulations and interactions with electrode factors are reported here, thus, no main effects of electrode factors (Lateralization and Anteroposterior) are shown. *Lat = Lateralization. Anteropost = Anteroposterior.

Mixed model ANOVA *Experiment 2*			
Group	$F = .02$	Group x Block x Lat	$F = 1.23$
(1,18)	$p = .881$	(4, 144)	$p = .302$
Block	**$F = 17.72$**	Block x Anteropost	$F = 2.09$
(2, 72)	**$p < .001$**	(2, 48)	$p = .133$
Group x Block	**$F = 3.98$**	Group x Block x	$F = 1.99$
(2, 72)	**$p = .024$**	Anteropost	$p = .144$
		(4, 144)	
Group x Lat	$F = .44$	Group x Lat x Anteropost	$F = .37$
(2, 72)	$p = .614$	(4, 144)	$p = .738$
Group x Anteropost	$F = .39$	Block x Lat x Anteropost	$F = .443$
(2, 72)	$p = .585$	(8, 288)	$p = .678$
Block x Lat	**$F = 7.62$**	Group x Block x Lat x	$F = 1.62$
(2, 72)	**$p < .001$**	Anteropost	$p = .200$
		(8, 288)	

Table 3
Results from the paired *t*-tests of *Experiment 2* for the mean N400 (350-550 ms) in the Cons Group. Results were corrected for multiple comparison applying FDR correction (corrected p value = .004). Bold results indicate the comparisons that survived at multiple comparison correction.

t-test *Experiment 2* Cons group			
Block 1 vs Block	$t(18) = -1.46$,	Block 2 vs Block	**$t(18) = -3.8$,**
2 (frontal ROI)	$p = .16$	3 (central ROI)	**$p = .001$**
Block 1 vs Block	**$t(18) = -3.88$,**	Block 1 vs Block	$t(18) = -3.27$,
3 (frontal ROI)	**$p = .001$**	2 (frontal ROI)	$p = .004$
Block 2 vs Block	**$t(18) = -3.44$,**	Block 1 vs Block	**$t(18) = -6.61$,**
3 (frontal ROI)	**$p = .003$**	3 (frontal ROI)	**$p < .001$**
Block 1 vs Block	$t(18) = -2.09$,	Block 2 vs Block	**$t(18) = -3.41$,**
2 (central ROI)	$p = .51$	3 (frontal ROI)	**$p = .003$**
Block 1 vs Block	**$t(18) = -5.32$,**		
3 (central ROI)	**$p < .001$**		

Table 4
Results from the paired *t*-tests of *Experiment 2* for the mean N400 (350-550 ms) in the Icons group. Results were corrected for multiple comparison applying FDR correction (corrected p value = .004). Note that none of the results survived the multiple comparison correction.

t-test *Experiment 2* Icons group			
Block 1 vs Block	$t(18) = .18$,	Block 2 vs Block	$t(18) = -2.54$,
2 (frontal ROI)	$p = .86$	3 (central ROI)	$p = .02$
Block 1 vs Block	$t(18) = -1.63$,	Block 1 vs Block	$t(18) = .229$,
3 (frontal ROI)	$p = .12$	2 (frontal ROI)	$p = .82$
Block 2 vs Block	$t(18) = -2.06$,	Block 1 vs Block	$t(18) = -2.24$,
3 (frontal ROI)	$p = .05$	3 (frontal ROI)	$p = .038$
Block 1 vs Block	$t(18) = .44$,	Block 2 vs Block	$t(18) = -2.51$,
2 (central ROI)	$p = .67$	3 (frontal ROI)	$p = .022$
Block 1 vs Block	$t(18) = -2.02$,		
3 (central ROI)	$p = .06$		

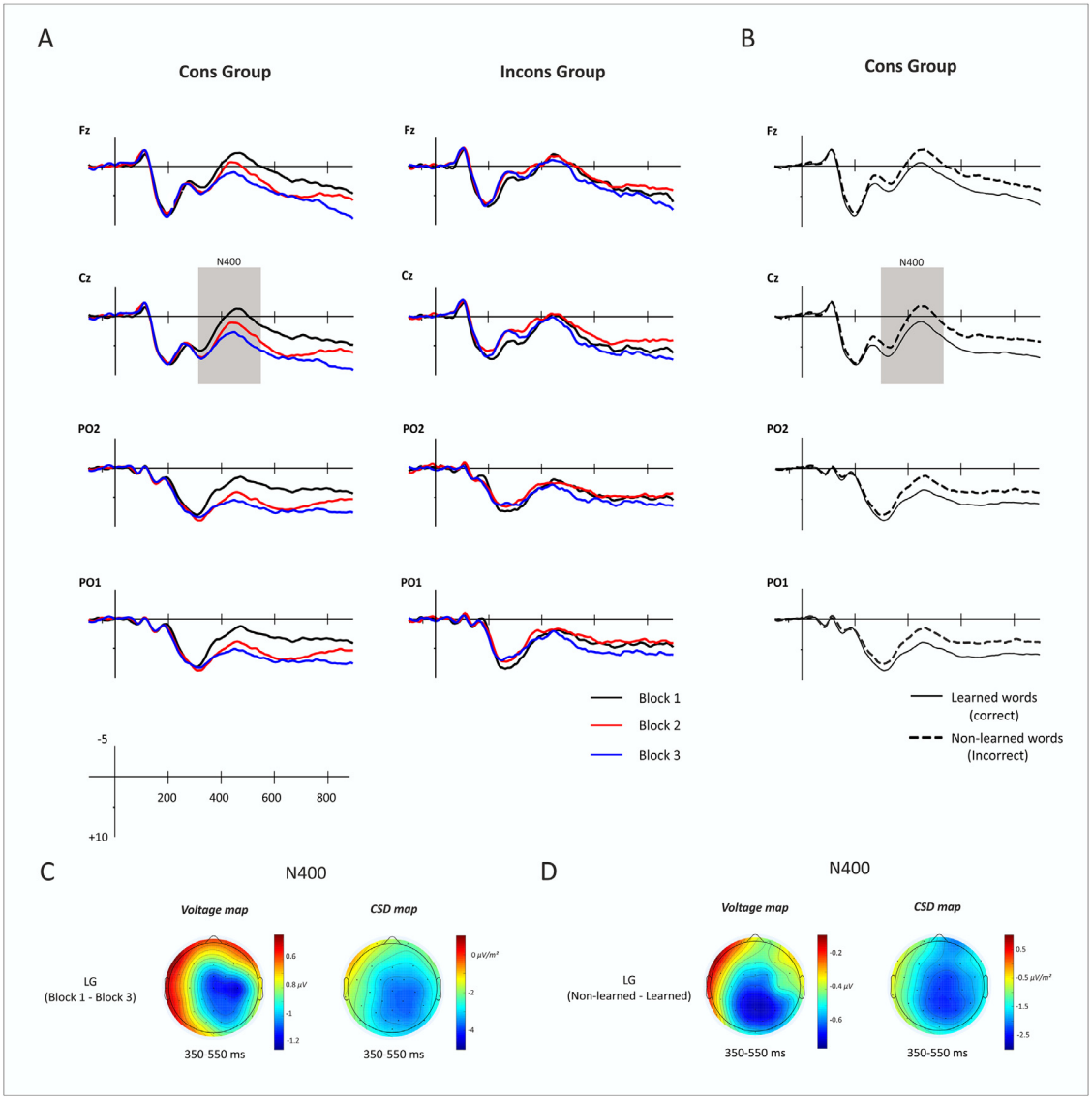


Fig. 6. A) Grand average ERPs to new pseudowords in both the Cons (left) and the Icons group (right) for each learning block. Notice that the N400 amplitude decreases across blocks in Cons but not in Icons. B) Grand average ERPs to pseudowords averaged across all blocks comparing correctly learned to non-learned pseudowords in the Cons group. C) Cons group: Scalp distribution and CSD maps of the mean N400 between 350 and 550 ms for the difference (Block 1 - Block 3) and D) the difference (Correct - Incorrect).

$F(1,18) = 36.82$; $p < .001$, see Fig. 6B]. We also found a significant Item x Lateralization interaction [$F(2,36) = 4.87$; $p = .021$]. The mean N400 effect (Incorrect – Correct) was maximal over central electrodes (-2.1 μV), which was confirmed by pairwise *t*-test showing a significantly larger effect over central than over left electrodes [$t(18) = 4.33$; $p = .001$, corrected for multiple comparisons]. However, no significant differences were found when comparing central to right electrodes [$t(18) = 1.74$; $p = .13$, corrected for multiple comparisons] and left to right electrodes [$t(18) = -0.97$; $p = .34$, corrected for multiple comparisons]. The N400 distribution for the difference waveform (Incorrect – Correct) was again centro-parietal in both the voltage and CSD maps (Fig 6D).

4. Discussion

This study examined the time course of early encoding and integration of new lexical information in human adults. We tracked associative learning between unfamiliar items and concomitant brain modulations from the early stages of learning up to the later stages. We also found significant relationships between associative learning (performance and ERP effects) and verbal fluency measures that tap cognitive control during lexical retrieval. Our study provides converging evidence for fast and slow neuroplasticity mechanisms supporting the learning of new information that may reflect the dynamic interplay between language-specific and domain-general brain resources.

Electrophysiological evidence for fast plastic changes was provided in the first experiment and replicated in the second one. In *Experiment 1*, novel pseudowords elicited a frontal N400 during the first block of the learning program (see Fig. 3A; 4A, 4B, right panel; and 6A left panel). This result confirms the findings of previous studies in adults using different experimental manipulations to show a larger N400 frontally distributed for learned compared to non-learned words or for newly learned words compared to familiar words (McLaughlin et al., 2004; Perfetti et al., 2005; Frishkoff et al., 2010; Mestres-Missé et al., 2007; Batterink and Neville, 2011; Yum et al., 2014; Dittinger et al., 2016; Stein et al., 2006; Bakker et al., 2015). Importantly, when comparing the first and last learning blocks of Day 1 (see Fig. 4A), we observed a within-session effect with a centro-parietal distribution. This was confirmed by the CSD transform of Fig. 4 showing the involve-

ment of a strong right-lateralized parietal sink together with a relatively weak frontal sink. This change in the topographical distribution of the N400 suggests the involvement of different neuronal resources across the learning process. Dittinger and colleagues (2016) reported a different pattern of N400 topographical modulations during word learning, with an increase of N400 amplitude from the first to the second learning block within-session over left and midline electrodes. Differences in the topographical distribution between the two studies may arise from differences in the task, and the stimuli used. While Dittinger's study (2016) used 90 association trials per learning block, we used 240 trials instead (pseudoword – new object trials). Thus the number of trials per learning block differed considerably between these experiments, having an impact on the granularity of the results and hindering early N400 modulations during the first block. Finally, this apparent discrepancy may reflect the fact that frontal regions were largely engaged during the initial stages of learning (Day 1). Indeed, in our study, no stored semantic information was available for the new referents. Therefore, frontal activations related to effortful semantic processing and retrieval were likely to occur during the early stage of training (Petersen et al., 1988; Demb et al., 1995; Ferstl et al., 2008; Badre and Wagner, 2002; Gold et al., 2006; Thomson-Schill et al., 1997).

We also found evidence for slow neuroplastic changes associated with automatization and long-term consolidation of new associations in *Experiment 1*. Specifically, we observed that the between-session learning effect (i.e., the difference in mean N400 amplitude between the first learning block of Day 1 and the average of all the learning blocks during Day 5, see Fig. 3A and 3B) had a clear frontal distribution that was even more focally distributed on the CSD transform (see Fig. 4B). Importantly, the mean N400 amplitude reached a plateau during Day 5, which may further suggest that the newly learned words had acquired robust and automatized lexical-semantic memory traces. Moreover, the increase in overt-naming performance, from low performance during the early stage of the training (11.5% in *Experiment 1* and 13.8% in *Experiment 2*) to quite high naming scores at the later stage of the training (74% during Day 5) supports this view. In the second experiment, we replicated the results of *Experiment 1* and found, again, a frontal N400 to novel words that decreased across learning blocks in the Cons group only despite a similar number of pseudoword repetition (Fig. 6A). Interestingly, N400 modulations across blocks were also observed in the Icons group, but failed to reach significance after correcting for multiple comparisons. The introduction of this additional group was important because, in this case, the participants were presented with fully inconsistent pseudoword-object associations where new pseudowords could not be systematically associated with any referent. This manipulation was crucial to disentangle the effects of repetition of information as opposed to encoding and word-to-referent mapping observed in Experiment 1 (see Cunillera et al., 2010 for a similar design with behavioural measures). Further, learned pseudowords elicited a smaller N400 than non-learned pseudowords in the Cons group (Fig. 6B). Although previous studies have shown that the N400 can be modulated by pseudoword repetition (Bermudez-Margaretto et al., 2018; Deacon et al., 2004), our results showed that the N400 is modulated by learning but not by repetition or familiarization, thus favor a lexical-semantic interpretation of the present N400 modulation (Bermudez-Margaretto et al., 2015, 2018, 2019; Kutas and Federmeier, 2000; Bakker et al., 2015). Overall, the results showing a modulation of the mean N400 across blocks in Day 1 of *Experiment 1* and those in the Cons group of *Experiment 2* suggest that semantic access was already taking place during the first day of training, probably due to a rapid learning process occurring during the initial acquisition of novel words (Rodriguez-Fornells et al., 2009).

An innovative aspect of *Experiment 1* was the 4-month follow-up that allowed us collecting the same behavioural data as in the 1-week training program. The results showed different patterns of performance in this evaluation. Specifically, participants presented low overt naming scores but performed above chance level in the 2AFC task. Importantly, these two tasks are known to tap on different processes: while overt-naming may rely on phonological retrieval and explicit recall, the 2AFC may involve familiarity judgment process. Therefore, our results suggest that the 4-month retention period differently impacted explicit recall and familiarity judgment processes, probably due to different sensitivity to long-term memory consolidation. Interestingly, we found an association between the frontal N400 between-sessions effect (block 1 of Day 1 minus average of Day 5) and the scores in the letter fluency task (see Fig. 5). Specifically, high scores of letter fluency were associated with a larger N400 between-sessions effect. The letter fluency task is known to rely heavily on phonemic abilities (Benton and Hamsher, 1976) to produce a word cued by a letter, and is supposed to mainly involve the left frontal regions (Gaillard et al., 2003; Andermaert et al., 2000; Abrahams et al., 2003). As the modulation of the N400 mean amplitude has been considered as a word learning index (McLaughlin et al., 2004; Mestres-Missé et al., 2007; Borovsky, Kutas and Elman, 2010), this result indirectly relates phonemic proficiency to novel pseudoword learning ability. Further, we found another significant association between semantic fluency and forgetting at 4 months, with higher fluency scores predicting lower forgetting (see Fig. 2C). As opposed to letter fluency, semantic fluency tasks rather rely on the left temporal system of semantic memory organization (Moscovitch et al., 1994; Pihlajamäki et al., 2000). Moreover, semantic fluency tasks require not only fast retrieval of words stored in the mental lexicon but also careful monitoring to select the appropriate words and avoid repetitions, i.e., cognitive control (Shao et al., 2014). Thus the significant association between semantic fluency and the forgetting index found here suggest that individual differences in lexical-semantic processing speed can predict long-term retention in novel word learning. Finally, even though some studies have shown a relationship between working memory and inhibitory control processes with second language learning performance (Kapa and Colombo, 2014; Linck and Weiss, 2015), we did not observe such associations. In children, cognitive control mechanisms are known to contribute to the early stages of contextual word learning (Hill and Wagovich, 2020). Further studies are needed to specify the relationships between phonemic and semantic fluency tasks and the behavioural and electrophysiological markers of verbal associative learning in adults.

The initial steps of word learning are arduous, and hence cognitive control and top-down processes such as voluntary attention and motivation are more likely to contribute to learning during these stages (Rodriguez-Fornells et al., 2009; Laine and Salmelin, 2010). It has been shown that lexical processing during word reading is top-down modulated by the intention to engage in the task at hand (Strijkers et al., 2015). However, a gradual automatization occurs when learning advances (Chein and Schneider, 2012). Interestingly, for an associative word learning task critically, this automatization depends on sleep (Tham et al., 2015). Such an automatization may be reflected by increased resistance to semantic interference during a semantic judgment task (Kazcer et al., 2018) and by an improvement in proficiency known to depend on the activity of the prefrontal cortex (Abutalebi, 2008; Jeon and Friederici, 2015). Here, participants were learning to associate new pseudowords to novel unfamiliar referents, which can also be considered as a conceptual learning task. Interestingly, both associative and concept learning processes rely on the activation of a complex network, including the prefrontal cortex and the hippocampus (Murray and Ranganath, 2007; Staresina and Davachi, 2009; Mack et al., 2020). Specifically, the medial part of the PFC contributes to the formation of long-term memory traces by favoring the binding of new information into already formed memory schemas (Tse et al., 2007; Van Kesteren et al., 2012).

Here, we found electrophysiological evidence for both fast and slow consolidation-related neural plastic changes as reflected in the mean N400, which supports the view of a stepwise emergence of new learning-based memory traces in adults, especially when no pre-existing semantic schemas could facilitate learning and consolidation processes (Havas et al., 2018). Importantly, our results also fit well with those of a recent behavioural study investigating the role of cognitive control

during the early stages of word learning (Hill and Wagovich, 2020). The authors showed the important role of cognitive flexibility in deriving the meaning of new words. Importantly, the results suggested that the trade-off between cognitive control and language learning mechanisms occurred differently depending upon the stages of word learning (early vs. late consolidation). With increasing learning instances, gradual consolidation of new memory traces may lead to more robust and precise lexical memory traces of the new words and their associations being integrated into the existing semantic networks and conceptual schemes. This may, in turn, lead to lexical and semantic retrieval of new words becoming faster and more resistant to interference with the involvement of cognitive control gradually diminishing inversely to retrieval automatization (Frischkoff et al., 2010; Chein and Schneider, 2005; 2012). A recent ERP study by Elgort and colleagues (2016) provided converging results supporting this idea. They investigated contextual word learning of a non-native language (L2). When dividing their sample into fast and slow second-language learners, the results showed a frontal N400 semantic priming effect that was also delayed around 150-200 ms in the slow learners. This result highlights the effortful nature of lexical-semantic retrieval of newly learned words, especially when learning has been weak (Elgort et al., 2015). Similar results were reported after one-shot learning exposure (Mestres-Missé et al., 2007), when learning new-words based on new phonological contrasts (Dittinger et al., 2016, 2017; Rasamimanana et al., 2020) or when no stored semantic are readily available to facilitate word learning (as it is the case in the present experiment).

Finally, some methodological limitations are worth considering. First, we analyzed N400 amplitudes using the mean activity during the canonical 350-550 ms time-window which does not allow exploring individual differences in N400 latency as done in previous studies using peak amplitude analyses (Elgort et al., 2016). Second, despite the use of CSD transforms known to increase the spatial resolution of the analyses, we gathered EEG with a limited number of electrodes and used only the qualitative aspects of these transforms. Third, despite evidence for successful recognition of object-pseudoword associations based on familiarity, the high forgetting rate observed in the follow-up evaluation does not fit well with the claim of automaticity. Further studies will be needed to understand better the dynamics of N400 modulations as well as to explore the cortical generators underlying the topographical transition from frontal to parietal locations across time. These studies will also be important to clarify the contribution of cognitive control mechanisms during both early and late stages of word learning.

5. Conclusion

We provide combined behavioural and electrophysiological evidence for the dynamics of acquiring new lexical information during encoding and consolidation, from the early stages of learning until the late phase after consolidation took place. Our data show stepwise emergence of newly learned lexical memory traces for which previously stored semantic schemas cannot directly facilitate learning and consolidation processes. These results favor an integrative view of language learning that involves a continuous interplay between language-specific and domain-general cognitive control brain networks.

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Authors contribution

NRE, CF, ML, and ARF planned the study. NRE, MSD, and DC performed the EEG measurements. NRE analyzed the data and performed the statistical analyses. NRE, CF, ML, and ARF contributed to the interpretation of the data and wrote the manuscript.

Data and code availability statement

The data that support the findings of this study are available on reasonable request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118443.

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