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Neuroplasticity in Visual Word Recognition: An Exploration of Learning-Related Behavioural and Neural Changes

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Neuroplasticity in Visual Word Recognition: An Exploration of Learning-Related Behavioural
and Neural Changes

by

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A THESIS

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Abstract

Visual word recognition is a cognitive process that remains relatively stable throughout adulthood. Despite this stability, recent research suggests that the system involved is malleable, by showing evidence of behavioural change after lexical decision task (LDT) practice, and of neural differences between-subjects during LDT performance. However, these studies leave the question unanswered as to whether neural *change* can occur within the visual word recognition system, which would suggest plasticity. We therefore investigated whether neural change accompanies the behavioural change previously found with LDT practice. If found, these neural changes could be due to processes associated with *learning*, where performance that is initially unskilled and effortful becomes skilled and efficient, and supported by a more specific, honed, and optimized task network. We replicated the British Lexicon Project (BLP), in which participants completed several days of LDT learning. We additionally recorded EEG at three time points to track neural change during LDT learning, and assessed event-related potentials and brain signal complexity. We found response time decreased during LDT learning, replicating the BLP. We also found neural change occurred through N170, P200, N400, and LPC amplitude effects, suggesting alterations to both the general cognitive and specific lexical processes involved in LDT performance. There was also widespread complexity decreases alongside localized increases, suggesting that with learning, LDT processing became more automatic with specific increases in processing flexibility. These findings suggest that the visual word recognition system is dynamic, flexible, and capable of undergoing plastic changes to support more efficient and automatic task performance.

Keywords: visual word recognition, plasticity, learning, lexical decision task (LDT), brain signal complexity, event-related potential (ERP)

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List of Acronyms and Abbreviations

BLP	British Lexicon Project
DLP	Dutch Lexicon Project
EEG	Electroencephalography
ERP	Event-Related Potential
ICA	Independent Component Analysis
LDT	Lexical Decision Task
LPC	Late Positive Component; Positive ERP component peaking around 600 ms post-stimulus
LV	Latent Variable
MSE	Multiscale Entropy
N170	Negative ERP component peaking around 170 ms post-stimulus
N400	Negative ERP component peaking around 400 ms post-stimulus
P200	Positive ERP component peaking around 200 ms post-stimulus
PLS	Partial Least Squares

Neuroplasticity in Visual Word Recognition: An Exploration of Learning-Related Behavioural and Neural Changes

Decoding a visual representation of a word and accessing its meaning, a process known as visual word recognition, is a human skill that is crucial to our ability to read and gain information from the world. Once we become literate, visual word recognition can be carried out with relative ease, automaticity, and incredible speed (e.g. Laszlo & Federmeier, 2014), often thousands of times each day. Despite the ease with which we carry out the task, from a neurocognitive perspective this skill is quite complex, as it depends on the coordination of many cognitive and perceptual processes. These include basic visual perception and eye movement control, orthographic, phonological and semantic processing, and the involvement of higher-level linguistic systems and aspects of memory that enable the derivation of meaning (Bentin et al., 1999; Norris, 2013).

The system involved in visual word recognition is considered to reach full development by early adulthood (e.g., Schröter & Schroeder, 2017; Sowell et al., 2003, 2004; Turkeltaub et al., 2003) and changes very little thereafter (Cohen-Shikora & Balota, 2016). Interestingly, despite this apparent stability, the visual word recognition system has shown signs of malleability. Recently, several studies known as Lexicon Projects have examined visual word recognition by testing healthy adult participants with large portions of the lexicon (between 14,000 and 40,000 words), and have assessed the effects of a number of variables on lexical decisions, providing insight into some of the most important factors in visual word recognition (Balota et al., 2007; Ferrand et al., 2010; Keuleers et al., 2010, 2012). The results of two of these studies, The Dutch Lexicon Project (DLP; Keuleers et al., 2010) and the British Lexicon Project (BLP; Keuleers et al., 2012), suggest that extensive practice with the lexical decision task (LDT)

can alter visual word recognition processes. Each study measured LDT response time as participants completed thousands of LDT trials across several days, and response time decreased over the course of practice, although more so in the BLP than the DLP. In a follow-up analysis of the BLP dataset, decreased effects of word frequency and imageability were among the practice-driven changes that resulted from making repeated lexical decisions (Hargreaves & Pexman, 2012). There is also evidence of visual word recognition system malleability from studies on expertise, specifically those involving Scrabble experts, as they have been found to respond faster than age-matched controls on LDT trials (Hargreaves et al., 2012; Protzner et al., 2016). An additional study found that higher levels of Scrabble expertise were associated with faster LDT reaction times, when controlling for age (Halpern & Wai, 2007). Together, these findings suggest that although the visual word recognition system is relatively stable in adulthood, it has the potential to be altered behaviourally in the context of learning through domain-specific practice.

What is less clear is whether the behavioural changes observed with LDT practice or extensive lexical experience are simply enhancements in performance, or if they extend to alterations of the neural substrates supporting visual word recognition. Previous between-subjects research has found some evidence in support of neural alterations with behavioural performance differences. For example, participants with high versus low levels of semantic reliance while reading showed variation in anterior temporal lobe and premotor region activity (Hoffman et al., 2015). Research involving Scrabble experts also provides some evidence: during LDT, Scrabble experts showed activation of bilateral regions involved in working memory and visual perception, while age-matched controls showed activation within more typical language regions (Protzner et al., 2016). For LDT with vertically oriented stimuli, Scrabble experts

showed an increased amplitude late positive component (LPC) compared to controls, which may signify improved stimulus evaluation and categorization afforded by experience (van Hees et al., 2017).

These findings provide some evidence of neural differences accompanying behavioural differences on word recognition tasks, but as this evidence comes from between-subjects comparisons, the conclusions that can be drawn about the nature of these changes are limited. To examine whether the behavioural changes associated with LDT or lexical practice, such as those observed in the BLP (Keuleers et al., 2012) or among Scrabble experts (Hargreaves et al., 2012; Protzner et al., 2016), are accompanied by neural changes, in the present study we utilized a within-subjects design and tracked behavioural *and* neural changes, using electroencephalography (EEG), across several days of LDT learning. If there are experience-related neural changes accompanying the behavioural changes previously found with LDT practice, this could occur through processes associated with *learning*. In general, when starting to learn to perform a completely new skill or task, performance is unskilled and effortful. In terms of learning associated with LDT or a similar visual word recognition task, literate adults already have expertise at identifying words, but as the LDT is not a typical, everyday task, performance at the beginning of learning will be less than optimal. As learning progresses, LDT performance becomes skilled and more efficient. Relating this to the neural underpinnings, sub-optimal performance early in learning tends to be supported by a neural network that has the ability to respond to novel task demands, but with continued practice and learning on the task, the network supporting task performance changes and becomes more specific, honed, and optimized (Petersen et al., 1998). In this sense, *learning* in the current study refers to the unconscious change in neural processes that come about due to experience gained in visual word recognition

through repeated performance of the LDT, rather than the more common use of the term referring to conscious acquisition of new knowledge or skills. In our study, we explored this possibility by looking at the changes that occur with LDT learning using event-related potentials (ERPs), and a newer metric, brain signal complexity, which reflects processing capacity in biological systems (McIntosh et al., 2008; Wang et al., 2016).

In terms of the ERP components of interest, if neural changes do occur with learning, we expected the changes would be evident in components related to processes involved in visual word recognition and LDT performance, namely orthographic and semantic processing, and stimulus evaluation and categorization (Balota et al., 1999; Bentin et al., 1999; Coltheart et al., 2001; Harm & Seidenberg, 2004; Norris, 2013). These are reflected in the N170, N400, and LPC. The N170, an early negative component peaking around 170 ms post-stimulus in occipito-temporal electrodes, has been associated with visual orthographic processing, with greater amplitudes observed in the left hemisphere for orthographic compared to nonorthographic stimuli (Bentin et al., 1999; Maurer et al., 2005; Simon et al., 2004).

Semantic processing has been associated with the N400, which is a negative component that peaks around 400 ms post-stimulus, typically in centro-parietal electrodes when examining effects of semantic ambiguity or improbability for written words in sentences (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). The N400 has also been related to the processing of meaning in general, with variable topography depending on the task and stimuli used (see Kutas & Federmeier, 2011 for review). Several studies have shown N400 effects in frontal scalp sites with lexical stimuli with, for example, concreteness and lexical manipulations (Barber et al., 2013; Kounios & Holcomb, 1994), ambiguity (Haro et al., 2017), repetition (Simon et al., 2004), and attention and semantic priming (Bentin, 1987; Bentin et al., 1985; McCarthy & Nobre,

1993). Due to the range of contexts in which N400 effects exist, researchers suggest this component could reflect processes related to lexical access, where reduced amplitudes are associated with easier lexical access (Bentin, 1987; Peeters, 2016), or more generally, ease of processing with regards to stimulus meaning, with reduced amplitudes representative of facilitated semantic processing (Kutas & Federmeier, 2011).

Lastly, stimulus evaluation and categorization have been associated with a late positive component (LPC) that peaks around 600 ms post-stimulus in central-posterior electrodes (Ito & Cacioppo, 2000; Polich & Donchin, 1988; Rugg, 1983; Yao & Wang, 2014), with decreased amplitudes found for task conditions requiring fewer attentional or cognitive resources, such as for congruent word pairs in priming studies (Herring et al., 2011; Hinojosa et al., 2009), categorically and evaluatively consistent stimuli (Ito & Cacioppo, 2000), and processing of concrete versus abstract words (Holcomb et al., 1999; Kounios & Holcomb, 1994; West & Holcomb, 2000). Overall, with learning on the LDT, we might expect to see changes in activation for some or all of these components, or possibly the additional activation of components not named here (Kelly et al., 2006).

As a second measure of brain function associated with learning, we examined brain signal complexity. The temporal fluctuations in brain signal have both stochastic and deterministic properties and thus are neither completely predictable nor entirely random. This structural richness should be thought of as *complex* rather than simply variable (Costa et al., 2002, 2005). We evaluated signal complexity using multiscale entropy (MSE), which measures the way signals behave over a range of temporal scales from fine (e.g., over 2 ms intervals) to coarse (e.g., over 40 ms intervals; Costa et al., 2002, 2005; McIntosh et al., 2008). If neural changes accompany behavioural changes with LDT learning, we expected the changes to be

evident through increases and/or decreases in MSE. In the literature on brain signal complexity and task performance, both higher and lower complexity have been linked with better or improved task performance.

Higher brain signal complexity has been associated with greater task accuracy (McIntosh et al., 2008; Mišić et al., 2010; Protzner et al., 2010, 2013; Wang et al., 2016), and more stable response times (McIntosh et al., 2008; Mišić et al., 2010). In addition, higher brain signal complexity has been associated with increases in the amount of information available for responding to a stimulus (Burles et al., 2019; Heisz et al., 2012, 2014; Mišić et al., 2010), because with increased information available about a stimulus, there may be engagement of a broader network of regions that presents as increased signal complexity. As the brain is a nonlinear and complex system, noise or signal complexity allows for the formation of and transition between different network configurations. With complexity present, the brain can quickly jump between different states or networks, meaning that the possible network configurations and repertoire available to the brain when responding to stimuli increase (Deco et al., 2011; McIntosh et al., 2010). In other words, increased complexity represents a greater repertoire available for responding to a stimulus, and in turn, this increased repertoire can be thought of as an enrichment of the processing involved in stimulus response or task performance.

Better task performance has also been associated with lower (i.e., more regular) brain signal complexity. Burles et al. (2019) found that participants responded faster and more accurately during a mental rotation task when stereoscopic disparity was present (vs. absent), and complexity was lower in frontal electrodes in this condition. The authors suggested that the lower complexity represented a decrease in cognitive load in frontal brain regions, which facilitated responding (Burles et al., 2019). Heisz et al. (2012) reported a decrease in signal

complexity and faster response times when stimulus presentation was immediately repeated. This decrease in neural response with stimulus repetition, often referred to as repetition suppression, can be explained in several ways (Heisz et al., 2012; for review, see Grill-Spector et al., 2006). For example, it could be due to a decreased firing rate of neurons in the task network (i.e., the fatigue model; Grill-Spector & Malach, 2001; Miller & Desimone, 1994); the extinction of response from neurons less essential in identifying the stimulus, with overall fewer neurons firing in the task network (i.e., the sharpening model; Desimone, 1996; Wiggs & Martin, 1998); or, faster processing of a stimulus, through shorter latencies or durations of neural firing within the task network (i.e., the facilitation model; Henson & Rugg, 2003). Therefore, decreases in signal complexity for a task may indicate that processing is becoming more automatic. Taking the sharpening model for example, with fewer, more essential neurons responding to the repeated stimulus, the decreased neural response could facilitate faster, more efficient, and more automatic processing (Grill-Spector et al., 2006) as the task network itself has been made simpler, thus becoming more specific and optimized.

In the context of the current study and visual word recognition, although behavioural performance may improve with LDT learning through reductions in response time, different parts of the task network may undergo changes related to enrichment or automatization of processing with learning, shown through increases and decreases in brain signal complexity. Although stimuli in the LDT are not repeated, the same types of stimuli appear throughout the task, and word and nonword responses are repetitive. Because the stimuli require processing from the same task network, effects similar to those occurring with repetition suppression could be observed, where, if a decrease in signal complexity is observed with LDT learning, neural response could become more simplified, with processing becoming more honed, optimized, and

automatic (Burles et al., 2019). At the same time, increases in brain signal complexity or enrichment of stimulus processing could be occurring in other areas of the brain, such that processing from certain areas increases as those areas become more important to making lexical decisions. Enrichment could also occur if there is an increase in the flexibility of the neural configurations that can be used when responding to a stimulus, such as when more information about a stimulus is available (Burles et al., 2019).

Therefore, to further understand neural change in LDT learning, in the current study we used an exploratory approach to investigate what the nature of neural changes might be if they are found to accompany the behavioural changes previously cited to occur after LDT learning. To do so, we replicated the BLP (Keuleers et al., 2012), in which participants completed 16 hours of LDT learning over an average period of one week. In order to track any potential neural changes to visual word recognition, we employed EEG to measure neural response at several time points throughout the LDT learning period: first, at the very beginning of learning to gain a baseline measure of neural response; second, just prior to midway through learning, as this was when the original BLP showed response time decreases began to stabilize; and third, at the end of the learning period to gain a final measure of neural response.

When analyzing our measures of neural response, we chose to analyze word and nonword trials together, as we were interested in the overall learning-related changes in LDT learning, rather than the changes that may occur for words or nonwords separately. We also expected that the cognitive processes learned would be similar for words and nonwords, as the diffusion model (Ratcliff, 1978; Ratcliff et al., 2004) suggests that both types of stimuli are evaluated according to the same processes during lexical decisions. For each lexical decision there is proposed to be a word and a nonword boundary, and during the decision process “wordness” evidence

accumulates towards the boundaries until there is enough evidence to reach one of the boundaries and the lexical decision can be made (Ratcliff et al., 2004).

We investigated two main questions regarding the behavioural and neural changes associated with LDT learning and malleability of the visual word recognition system. First, we examined whether or not we could replicate the behavioural findings of the BLP. That is, as LDT learning progresses, will response time decrease? Based on the BLP (Keuleers et al., 2012), we expected response times to decrease between the first and second EEG measurement points, and then level off from the second to third EEG measurement points. Second, we examined whether or not these experience-driven behavioural changes were accompanied by neural changes. To explore the potential neural effects of LDT learning, we performed exploratory analyses of ERPs and MSE to see if neural response changed throughout the learning period. As discussed above, in the ERPs, we expected learning-related changes (increases and/or decreases in activation) to be associated with visual orthographic processing (N170), semantic processing (N400), and stimulus evaluation and cognitive resource allocation (LPC), possibly in addition to other components. For the measure of brain signal complexity, we expected MSE to show changes related to an enrichment of processing, where MSE would increase with learning, and/or to change in such a way that processing would become more automatic, where MSE would decrease with learning.

Method

Participants

Twenty-one healthy adults (10 females) participated as part of a larger study. Participants ranged in age from 20 to 28 years ($M = 23.90$, $SD = 2.86$), and had 13 to 24 years of education ($M = 17.48$, $SD = 2.75$). Participants were recruited through word of mouth by the researchers.

This was done to ensure quality of task completion as well as to reduce the likelihood of participant attrition. Criteria for inclusion were right-handedness, having normal or corrected-to-normal vision, and speaking English as a first language; seven participants additionally reported having a second language. Exclusion criteria included having a history of neurological disease or disorder, mental illness, head trauma, alcohol or drug abuse, or use of psychotropic medications within the last two years. Ethics approval was obtained from the Conjoint Faculties Research Ethics Board of the University of Calgary, and the study was conducted in accordance with all relevant guidelines and regulations. All participants provided written informed consent before taking part in the study and were provided with monetary compensation for their participation.

In the current study, we used a sample size of 20 participants, as this size is typically used to ensure sufficient power for EEG studies (Luck, 2014a). Admittedly, larger samples have been used for behavioural studies, but our within-subjects design and the extremely large number of trials completed per participant (1,500 per EEG session) should mitigate any potential sample size issues in the behavioural realm.

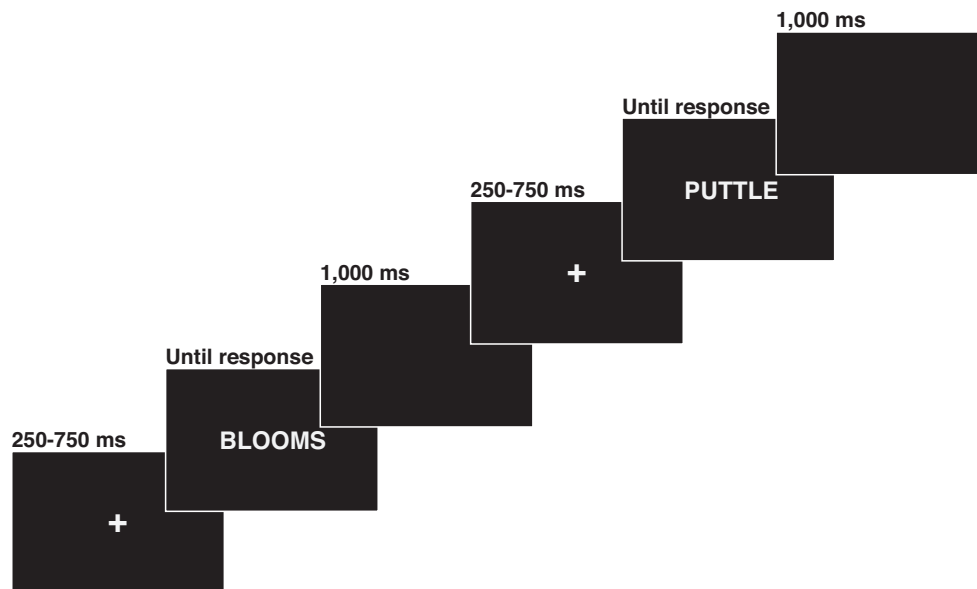
Stimuli

Word stimuli were obtained from the BLP (Keuleers et al., 2012). From the total list of 14,365 word stimuli, words were selected for the present study if they were 3-8 letters in length and elicited response accuracy greater than 10% in the BLP study. Word stimuli meeting these criteria were divided into 40 blocks of 250 items (10,000 words total), and were matched across blocks for frequency (British National Corpus, <http://www.natcorp.ox.ac.uk>), orthographic neighbourhood density (Coltheart et al., 1977), orthographic Levenshtein distance (Yarkoni et al., 2008), number of letters, and number of syllables. The 10,000 word stimuli were then used to generate the same number of nonwords using Wuggy, a pseudoword generator (Keuleers &

Brysbaert, 2010). The nonwords were matched to the words in each block on length, morphological structure, syllabic and sub-syllabic structure, and transition frequencies of the sub-syllabic segments. Monosyllabic nonwords differed from the target words on one sub-syllabic segment (onset, nucleus, or coda), whereas disyllabic nonwords differed on two sub-syllabic segments. As with the words, the nonwords were divided into 40 blocks of 250 items, with one nonword block assigned to each of the word blocks, creating 40 blocks of 500 items (250 words, 250 nonwords). Nine blocks were assigned to the EEG sessions, and the remaining 31 blocks were assigned to the online sessions.

LDT Learning Procedure

The learning period consisted of 40 blocks (500 trials per block) of a visual LDT, with the order of blocks randomized for each participant. Learning was spread over 16 hours within a one-week period. Throughout the learning period, participants were asked to maintain at least 80% accuracy on the LDT blocks. Each trial began with the presentation of a central fixation cross on a computer screen for a jittered duration of 250-750 ms ($M = 500$ ms), followed by the stimulus. Stimuli were presented one at a time in uppercase white typeface on a plain black background. Participants were asked to respond as quickly and accurately as possible by pressing the 'D' key with their left index finger for a nonword response, or the 'K' key with their right index finger for a word response. The stimulus remained on screen until a response was made. Following the response, a 1,000 ms blank screen appeared, followed by the start of the next trial. Self-paced break screens appeared every 100 trials, and participants were instructed to indicate by key press when they were ready to continue. At the end of each block of 500 trials participants were provided with accuracy feedback. Figure 1 shows an outline of the LDT learning procedure.

Figure 1*Lexical Decision Task (LDT) Stimulus Presentation*

Note. Example stimuli and outline of stimulus presentation in the lexical decision task (LDT).

Participants made decisions as to whether letter strings were words or nonwords, with a central fixation cross presented before each trial and a blank screen presented after each trial. A self-paced break screen also appeared every 100 trials.

Learning Blocks with Simultaneous EEG Recording

At three time points, participants completed LDT learning with simultaneous EEG recording in the lab: at the beginning of the learning period (Blocks 1 to 3), prior to midway through learning (Blocks 16 to 18), and at the end of learning (Blocks 38 to 40). EEG session timing was chosen based on the response time changes reported in the BLP, with a decrease in response time expected between the first and second EEG sessions, and a leveling off of response time between the second and third EEG sessions (Keuleers et al., 2012). The LDT learning program was presented to participants, following the procedure described above, on a

24-inch monitor using Presentation software (Version 16.1, Neurobehavioural Systems, Inc.).

Participants were seated approximately 80 cm from the computer screen and the visual angle of the LDT stimuli ranged from $2.4 \times 0.6^\circ$ for three-letter strings to $6.4 \times 0.6^\circ$ for eight-letter strings. In addition to EEG recording, response time and accuracy were recorded.

Online Learning Blocks

The remainder of LDT learning was completed outside of the lab. As the order of blocks was randomized for each participant, links to each LDT learning block were emailed to participants in the specific order in which they were to be completed. The learning program was presented to participants online via Qualtrics following the LDT learning procedure outlined above. All participants completed 12 learning blocks between the first and second EEG sessions, and 19 learning blocks between the second and third EEG sessions. Only accuracy was recorded during these blocks, as differences in internet connection speeds may have influenced response times.

EEG Recording and Pre-Processing

EEG data were acquired in a dimly lit, radio frequency shielded and sound attenuated chamber. Continuous EEG was recorded from 64 electrodes (Cz as reference) at a 500 Hz sampling rate with a band-pass of 0.05-100 Hz. An EasyCap (10/20 positioning system) and Brain Vision actiCHamp system with active electrodes (Brain Products GmbH) was used, and all electrode impedances were below 17 k Ω at the start of recording. Raw data were then band-pass filtered at 0.1-55 Hz and re-referenced to an average reference. Artefact removal was completed in EEGLAB (Version 14.1.2; Delorme & Makeig, 2004) using independent component analysis (ICA). ICA decomposition was performed, and components carrying muscle artefacts or ocular artefacts (i.e. eye blinks, saccades, horizontal eye movements) were removed. Data were

segmented into epochs from 200 ms pre-stimulus onset to 1,000 ms post-stimulus onset, and baseline corrected to the 200 ms pre-stimulus interval. Correct trials from both task conditions (i.e., words and nonwords) were then averaged for each participant for each EEG session.

Behavioural Analyses

We analyzed behavioral data to assess whether our results replicated the learning effects for word and nonword responses in the original BLP (Keuleers et al., 2012, illustrated in their Figure 1). In these analyses only, we analyzed word and nonword trials separately to allow for a direct comparison with the BLP analyses. To do so we analyzed response time and accuracy with 2 (lexicity: word, nonword) by 3 (EEG session: Session 1, Session 2, Session 3) repeated measures ANOVAs. For any resulting significant interactions, follow-up analyses of simple main effects were conducted.

Electrophysiological Analyses

Correct trials for all stimuli (i.e., words and nonwords) were combined and analyzed in two ways. Word and nonword trials were combined in these analyses as we were interested in the learning-related changes that occurred during LDT as a whole, rather than in those that occurred for a specific type of stimuli. First, to facilitate analysis of ERP and MSE changes *across* the three EEG sessions (i.e., Session 1 vs. 2 vs. 3), correct trials for each participant for each of the three EEG sessions were averaged within participant. This provided ERP and MSE measures of the average neural response for each EEG session.

Second, to facilitate analysis of ERP and MSE changes *within* the EEG sessions, for each participant the correct trials from an EEG session were examined across each of 10 segments in a session. That is, each segment contained a consecutive 10% of the trials from the respective session for each participant, and the trials for each segment were averaged within participant. For

example, if a participant had 950 correct trials in EEG Session 1, Segment 1 would contain trials 1-95, Segment 2 would contain trials 96-190, ... Segment 10 would contain trials 856-950. If the total number of correct trials was not evenly divisible by 10, the remainder was added by 1 to the first x segments equivalent to the value of the remainder (e.g., if the remainder was 3, Segments 1-3 would contain one extra trial each, compared to Segments 4-10). This provided ERP and MSE measures of the average neural response for each segment within an EEG session, and enabled the examination of changes within an EEG session.

Event-Related Potentials (ERPs)

ERPs were computed to obtain a measure of the average electrical activity of the brain in response to the stimuli (i.e., the brain response during the process of making lexical decisions). To obtain ERPs, we used the ERPLAB toolbox (Version 7.0.0; Lopez-Calderon & Luck, 2014) within the EEGLAB software (Version 14.1.2; Delorme & Makeig, 2004) available for MATLAB (R2014a). ERPs were computed for each participant at each electrode, and then were analyzed according to the two methods described above using partial least squares analysis (described below).

Multiscale Entropy (MSE)

Multiscale entropy (MSE) was used to estimate brain signal complexity, and was calculated in MATLAB (R2014a) using the algorithm available at <https://www.physionet.org/content/mse/> (Costa et al., 2002, 2005; McIntosh et al., 2008). A detailed description of MSE and its applicability in analyzing signal complexity is available in Costa et al. (2002, 2005). To summarize, the MSE algorithm calculates sample entropy as a measure of the predictability (or regularity) of the signal at different timescales. This happens in two steps.

The first step involves resampling the data to create 22 discrete timescales. For each scale, data points within non-overlapping windows were averaged together. For example, the original time series was Scale 1 (i.e., 2 ms windows in the context of our 500 Hz sampling rate), Scale 2 averaged over 2 non-overlapping time points (i.e., 4 ms windows), up until Scale 22 (i.e., 44 ms windows).

The second step involves calculating sample entropy for each timescale. This is done by measuring the regularity of corresponding time series by evaluating the probability of repetitive patterns based on two parameters: the pattern length m and the tolerance level or similarity criterion r . In the current study, the pattern length ($m = 2$; McIntosh et al., 2008) means two consecutive data points were used for pattern matching. Sample entropy therefore reflects the probability that two sequences that match on the first two data points also matched on the next data point. The tolerance level ($r = .50$; McIntosh et al., 2008) means that for two data points to be considered matching, the absolute amplitude difference between the two data points should be less than or equal to 50% of the original time series standard deviation.

For the current study, electrode-specific MSE was calculated for each participant on single trials and then averaged across all trials within a given condition (i.e., either averaged across all trials for an EEG session, or averaged across trials within a segment of an EEG session).

Partial Least Squares (PLS) Analysis

To analyze the ERP and MSE data, partial least squares (PLS) analysis was used in MATLAB (R2014a; <http://www.rotman-baycrest.on.ca/index.php?section=345>; McIntosh et al., 1996). PLS is a data-driven multivariate analysis technique that operates on the entire data structure at once, identifying patterns of maximal covariance between ERPs/MSE and conditions

across all electrodes and timescales simultaneously. This is an optimal method to analyze the ERP and MSE data since the goal of this study is to examine changes in ERP amplitudes and MSE across the scalp, without any a priori electrodes of interest. Further details of PLS can be found in prior literature (Krishnan et al., 2011; Lobaugh et al., 2001; McIntosh et al., 2008; McIntosh & Lobaugh, 2004).

The current study used a task PLS analysis. In task PLS, latent variables (LVs) showing similarities or differences between experimental conditions are identified. Task PLS is similar to principal components analysis, as a priori contrasts across conditions are not specified. Instead, the algorithm extracts orthogonal LVs based on the amount of covariance explained between conditions and neural activity, with LVs extracted in order of highest to lowest amount of covariance explained. Each extracted LV contains three vectors that represent design saliences, electrode saliences, and the singular value. Design saliences identify a contrast of the similarities and differences between conditions. Electrode saliences identify a particular pattern of electrodes and timescales that are most related to the condition difference expressed in the LV. The singular value represents the strength of the effect expressed by the LV, i.e., the proportion of covariance accounted for.

To assess the statistical significance and reliability of the LVs identified with PLS, permutation tests and bootstrapping were performed. The permutation test assesses whether the effect represented in a given LV is strong enough to be considered different from random noise. This test involves reassigning the order of conditions for each subject (with the order of subjects remaining fixed) and recomputing PLS on the permuted data. We ran 500 permutations, so that a probability value would be derived from the number of times out of 500 that the singular value

from each permuted data set is greater than or equal to that of the original data. If this probability is very low ($p < .05$) the LV is considered significant.

Bootstrapping assesses the reliability of the electrode-timepoint contributions by reassigning subjects to the conditions (with the order of conditions remaining fixed). This assesses the reliability of non-zero electrode saliences within significant LVs. The electrode salience is considered to be reliable if the salience value is not dependent on which combination of subjects are included in each sample. Using this method, corrections for multiple comparisons are not necessary because the electrode saliences are calculated in a single mathematical step. The bootstrap ratio is proportional to a z score, but should be interpreted as a confidence interval. We used 500 bootstrap samples and a minimum threshold of 2.0, which corresponds to a 95% confidence interval, or a p value $< .05$. In some analyses, we used a higher bootstrap threshold as necessary to best illustrate the effects, which corresponds to an even lower p value.

Results

All participants completed the LDT learning blocks in 6 to 10 days ($M = 6.75$, $SD = 1.07$). One participant was excluded from analyses for failing to maintain the minimum 80% accuracy during the LDT learning blocks, leaving $N = 20$ (age = 20-28 years, $M = 23.70$, $SD = 2.77$; education = 13-23 years, $M = 17.15$, $SD = 2.37$). For the accuracy analyses, trials with response times ± 2.5 standard deviations from the mean of each condition for each participant were excluded (2.5% of all data). For the response time and neural analyses, trials with response times ± 2.5 standard deviations from the mean of each condition for each participant were excluded (2.5% of all data), as well as trials with incorrect responses (12.3% of all trials).

Behavioural Results

Analyses for response time and accuracy were conducted in R software (Version 1.1.456) using the packages “ez” (Lawrence, 2016) and “rstatix” (Kassambara, 2020). Behavioural analyses were two-tailed with an alpha level of .05, unless otherwise indicated. Assumption of normality was tested with the Shapiro-Wilk test, and the assumption was met ($p > .05$) unless otherwise stated. Sphericity was tested with Mauchly’s test, and the assumption was met ($p > .05$) unless otherwise stated, in which case the Greenhouse-Geisser correction was applied. Table 1 provides the means and standard deviations for response time and accuracy measures for the three EEG sessions.

Table 1

LDT Learning Response Time and Accuracy for Word and Nonword Trials

	Response Time (ms)		Accuracy (proportion correct)	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Words				
Session 1	811.16	123.41	.87	0.04
Session 2	763.96	120.24	.86	0.04
Session 3	727.24	103.49	.86	0.04
Nonwords				
Session 1	924.97	185.92	.92	0.07
Session 2	824.87	136.99	.94	0.03
Session 3	778.75	115.08	.93	0.04

Note: $N = 20$.

Response Time

Figure 2a shows mean response time by EEG session and lexicality. There was a significant main effect of lexicality, $F(1, 19) = 25.33, p < .001, \eta^2_G = .08$, a significant main effect of EEG session, $F(2, 38) = 10.90, p < .001, \eta^2_G = .12$, and a significant interaction between lexicality and EEG session, $F(1.19, 22.65) = 6.27, p = .016, \eta^2_G = .01$ (Greenhouse-Geisser correction applied).

To parse this interaction, response times for the three EEG sessions were analyzed separately for words and nonwords (see Figure 2a). For words, there was a significant main effect of EEG session, $F(2, 38) = 7.00, p = .003, \eta^2_G = .08$. Follow-up paired samples t -tests ($\alpha = .017$) indicated a significant decrease in response time from Session 1 to Session 3, $t(19) = 3.58, SE = 23.43, p = .002, d = 0.80$, with nonsignificant differences between Sessions 1 and 2, $t(19) = 1.80, SE = 26.22, p = .088, d = 0.40$, and between Sessions 2 and 3, $t(19) = 2.19, SE = 16.77, p = .041, d = 0.49$. For nonwords, there was a significant main effect of EEG session, $F(1.46, 27.79) = 12.14, p < .001, \eta^2_G = .15$ (Greenhouse-Geisser correction applied). Follow-up paired samples t -tests ($\alpha = .017$) indicated a significant decrease in response time from Session 1 to Session 2, $t(19) = 2.84, SE = 35.30, p = .011, d = 0.63$, and between Sessions 1 and 3, $t(19) = 4.31, SE = 33.91, p < .001, d = 0.96$, but not between Sessions 2 and 3, $t(19) = 2.41, SE = 19.11, p = .026, d = 0.54$.

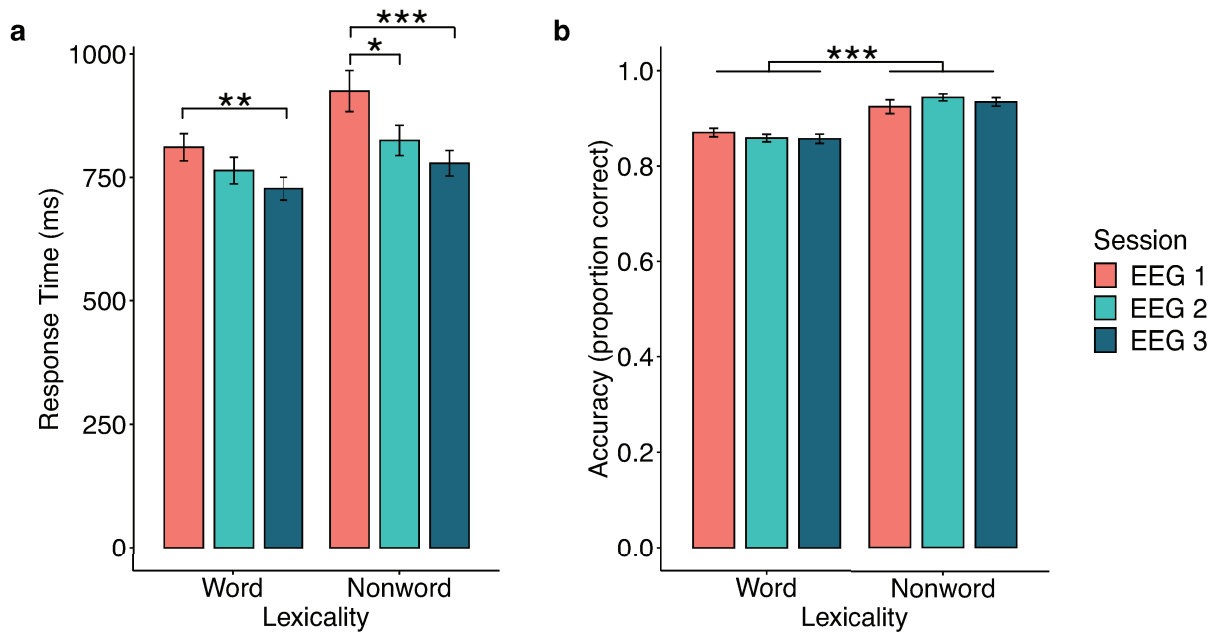
Accuracy

Figure 2b shows mean accuracy by EEG session and lexicality. Normality was violated in three data subsets: Session 1 nonwords, $W(19) = 0.82, p = .002$; Session 2 nonwords, $W(19) = 0.85, p = .005$; Session 2 words, $W(19) = 0.88, p = .015$. However, due to the lack of an appropriate nonparametric alternative for factorial repeated measures ANOVA, and in order to

more directly compare these results with those of the BLP, we maintained use of the parametric factorial repeated measures ANOVA. There was a significant main effect of lexicality, $F(1, 19) = 34.06, p < .001, \eta^2_G = .41$, where responses to nonwords were more accurate than to words ($M = .93, SE = .01$ vs. $M = .86, SE = .01$; see Figure 2b). The main effect of EEG session ($F(2, 38) = 0.74, p = .484, \eta^2_G = .003$) and the interaction between lexicality and EEG session ($F(1.39, 26.35) = 2.26, p = .138, \eta^2_G = .02$; Greenhouse-Geisser correction applied) were both nonsignificant.

Figure 2

Behavioural Effects of LDT Learning



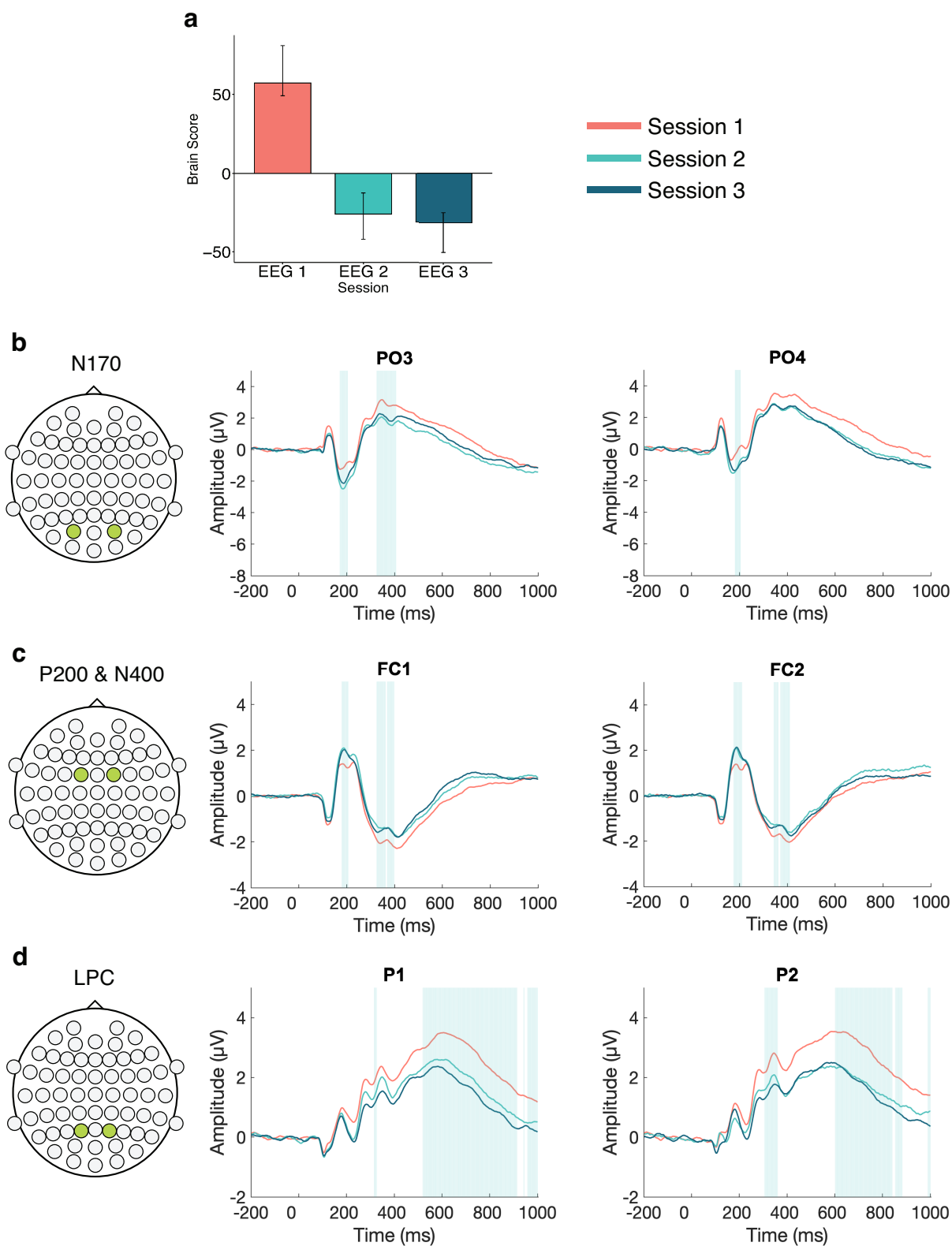
Note. (a) Response time decreased significantly for both words and nonwords from Session 1 to Session 3, and from Session 1 to Session 2 for nonwords. (b) Responses to nonwords were significantly more accurate than to words across learning. Error bars represent 1 standard error.

* $p < .05$, ** $p < .01$, *** $p < .001$.

EEG Results

Event-Related Potentials

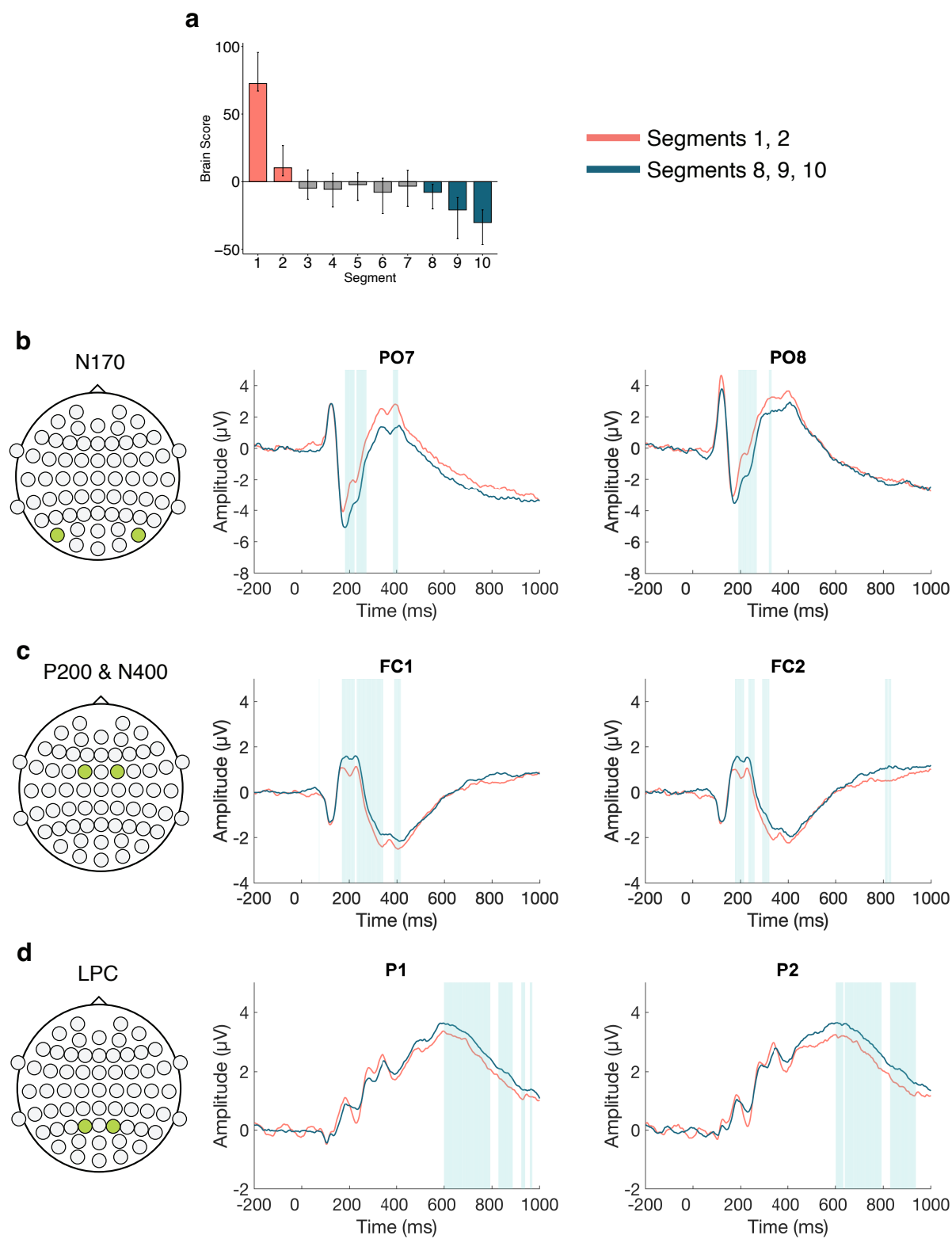
Across Session ERPs. A task PLS analysis was performed on ERPs for correct word and nonword trials combined, and resulted in one significant LV ($p < .001$; Figure 3). This LV revealed a difference between Session 1 versus Sessions 2 and 3, with no difference between Sessions 2 and 3. The analysis highlighted four ERP components, the N170, P200, N400, and LPC. As LDT learning progressed, the N170 amplitude became more negative from Session 1 to Sessions 2 and 3. This difference was stable between 175-205 ms in bilateral occipito-parietal electrodes. The P200 and N400 amplitudes became more positive from Session 1 to Sessions 2 and 3. For the P200, this difference was stable between 175-205 ms in bilateral frontal and fronto-central electrodes. For the N400, this difference was stable between 370-405 ms in bilateral frontal and fronto-central electrodes. The LPC showed a similar pattern as the N170, where the amplitude became more negative from Session 1 to Sessions 2 and 3. This difference was stable between 550-1,000 ms in bilateral centro-parietal and parietal electrodes.

Figure 3*Across Session ERP Results*

Note. Electrodes shown are representative of each effect. Highlighted areas in the ERP waveforms indicate the time points when the difference was reliable. (a) Task PLS analysis differentiated between Session 1 versus Sessions 2 and 3. Error bars represent 95% confidence intervals. (b) N170 showing more negative amplitude later in learning. (c) P200 (first highlighted area) and N400 (second highlighted area) showing more positive amplitude later in learning. (d) LPC showing less positive amplitude later in learning. Head plots in (b), (c), and (d) indicate locations of electrodes shown.

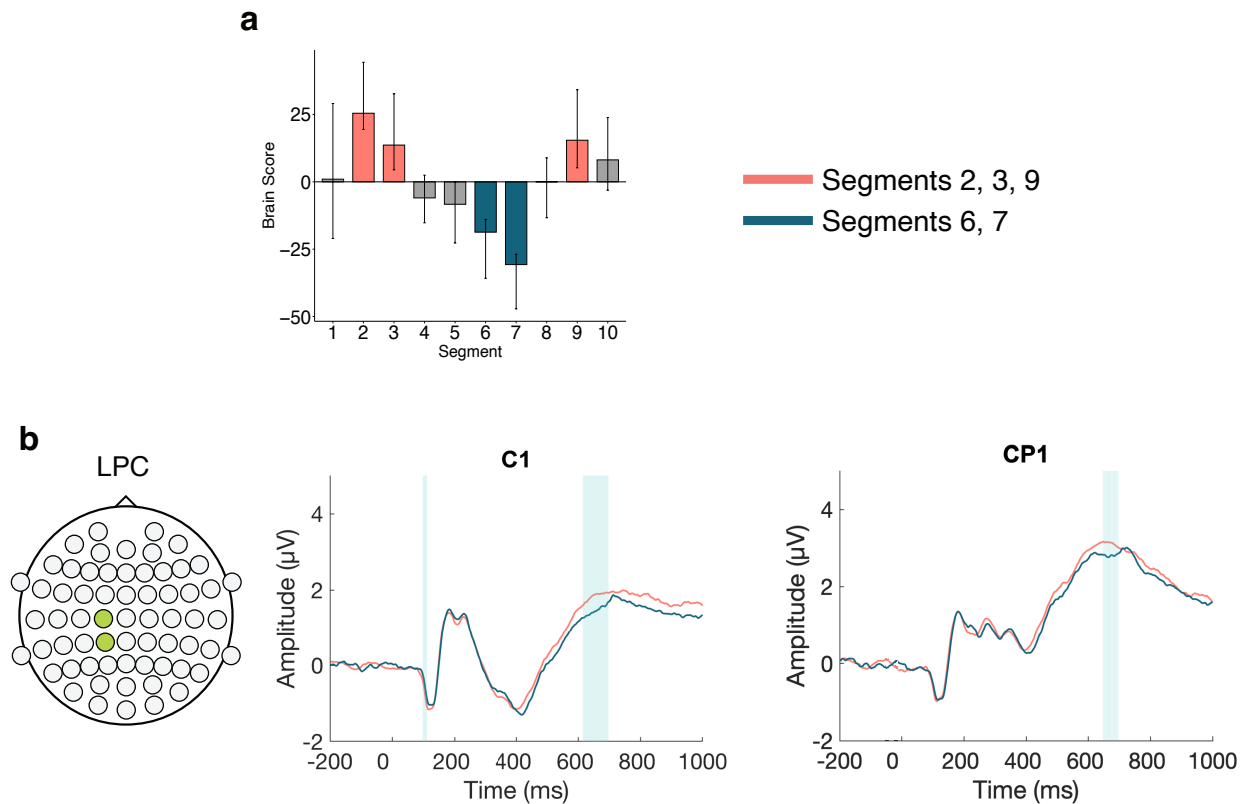
Within Session ERPs. As the across session results showed that the ERP changes occurred from Session 1 to Session 2, suggesting that most of the learning-related changes happened within the first session, we examined the changes that occurred over time during Session 1 in more detail. Results from Sessions 2 and 3 are only described as supplemental information to the Session 1 results. A task PLS was performed on ERPs for correct trials, divided into 10 segments of approximately 100 trials each, for each participant, from Session 1. This analysis resulted in two significant LVs. The first LV ($p < .001$; Figure 4) identified a difference between the beginning of the session (Segments 1, 2) and the end of the session (Segments 8, 9, 10). Four ERP components were highlighted by the analyses; the N170, P200, N400, and LPC. The N170 amplitude became more negative from the beginning to the end of the EEG session. This difference was stable between 170-215 ms in bilateral occipito-parietal electrodes. The P200 amplitude became more positive later in the session compared to the beginning, with the difference being stable between 180-210 ms in bilateral frontal, fronto-central, and central electrodes. Similarly, the N400 amplitude increased from the beginning to the end of the session. This difference was stable between 390-410 ms in left frontal and fronto-

central electrodes and bilateral central electrodes. The LPC amplitude also became more positive later in the session compared to the beginning of the session, and this difference was stable between 600-800 ms in bilateral centro-parietal and parietal electrodes.

Figure 4*Within Session ERP Results for Session 1 (LV 1)*

Note. Electrodes shown are representative of each effect. Highlighted areas in the ERP waveforms indicate the time points when the difference was reliable. (a) Task PLS analysis differentiated between the beginning and end of Session 1. Error bars represent 95% confidence intervals. (b) N170 showing more negative amplitude later in the session. (c) P200 shown in left and right panels, with more positive amplitude later in the session; N400 shown in left panel only, which had left-lateralized effects, with more positive amplitude later in the session. (d) LPC showing more positive amplitude later in the session. Head plots in (b), (c), and (d) indicate locations of electrodes shown.

The second LV ($p = .004$; Figure 5) differentiated between the beginning and end of the session (Segments 2, 3, 9) and the middle of the session (Segments 6, 7). The analysis revealed that LPC amplitude decreased (became less positive) in the middle of the session, compared to the beginning and end. This difference was stable between 615-700 ms at mainly left central and centro-parietal electrodes.

Figure 5*Within Session ERP Results for Session 1 (LV 2)*

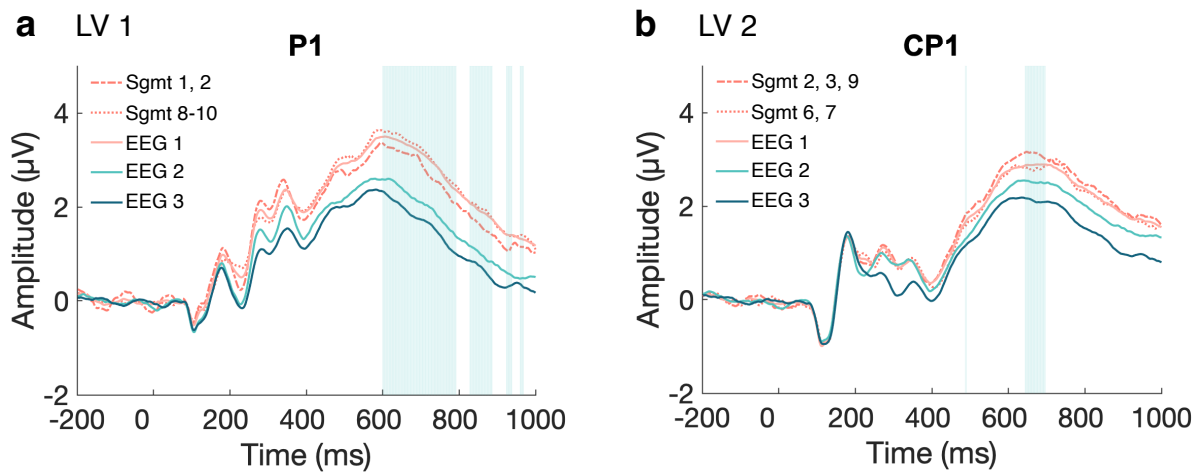
Note. Highlighted areas in the ERP waveforms indicate the time points when the difference was reliable. (a) Task PLS analysis differentiated between the beginning and end compared to the middle of Session 1. Error bars represent 95% confidence intervals. (b) LPC showing more negative amplitude in the middle of the session. Electrodes shown are representative of the effect, which was left-lateralized. Head plot indicates locations of electrodes shown.

Because the patterns of change for the LPC were different within Session 1, we examined Session 2 and Session 3 to see if an LPC effect was present and if it compared with what occurred during Session 1. An effect was not found; however, this is in line with the across session results showing that the majority of learning-related changes occurred during the first

session. Although the second LV in Session 1 showed decreased LPC amplitude in the middle of the session, overall the results showed that the LPC amplitude increased during learning within Session 1, due to the increase observed in the first LV (Figure 6a), and the increase from the middle to end of the session in the second LV (Figure 6b).

Figure 6

Comparison of LPC Waveforms Within Session 1



Note. LPC waveforms for LV 1 (a) and LV 2 (b) within Session 1, with across session waveforms included to depict amplitude change within Session 1 compared to the average amplitudes across the three EEG sessions. (a) LPC amplitude is lower at the beginning of the session (dashed line), but still more increased compared to Sessions 2 and 3, and then is increased at the end of Session 1 (dotted line). (b) Within Session 1, initially LPC amplitude is increased (dashed line) and then decreases in the middle of the session (dotted line), although the amplitude remains greater than the average amplitude in Sessions 2 and 3, and then increases again at the end of Session 1 (dashed line).

Brain Signal Complexity

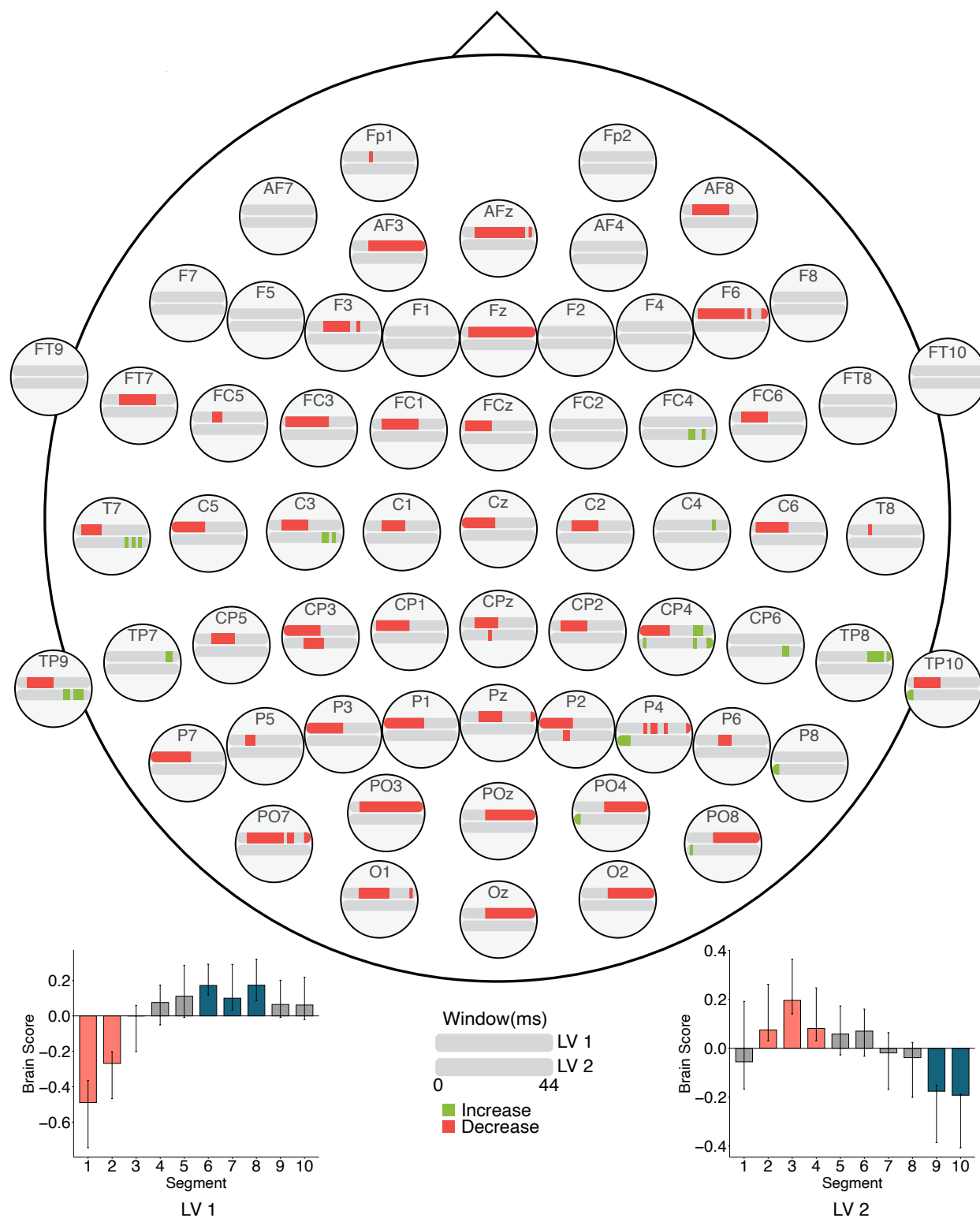
Across Session MSE. A task PLS analysis was performed on MSE calculated for correct trials, and resulted in one significant LV ($p < .01$; Figure 7). Similar to the ERP analysis, this LV also identified a difference between Session 1 versus Sessions 2 and 3. Later in learning (i.e., Sessions 2 and 3) there were decreases in fine to medium scale MSE (2-30 ms windows) in right fronto-central and left posterior electrodes, as well as fine to coarse scale MSE decreases (10-44 ms windows) in a few bilateral frontal electrodes. In addition, there were localized increases in coarse scale MSE (30-44 ms windows) in Sessions 2 and 3 compared to Session 1, in right parietal electrodes.

Note. Bar colour indicates direction of effect, with red indicating decreases in MSE, green indicating increases in MSE, and grey indicating no reliable effect. Plot in the top right indicates

the differences in MSE were found between Session 1 versus Sessions 2 and 3. Error bars represent 95% confidence intervals.

Within Session MSE. As with the ERPs, we chose to examine the changes that occurred over time during Session 1 in more detail, since the across session results showed that the MSE changes occurred from Session 1 to Session 2. A task PLS analysis was performed on MSE calculated for correct trials, for the 10 segments of trials in the first EEG session, and resulted in two significant LVs (Figure 8). The first LV ($p < .001$) identified a difference between the beginning of the EEG session (Segments 1, 2) and the middle/end of the EEG session (Segments 6, 7, 8). This pattern revealed that MSE decreased across the scalp towards the middle/end of the session in fine to medium scales (2-24 ms windows) throughout the brain, and there were also a few localized decreases in coarse scale MSE (10-44 ms windows) in mainly central and right frontal, parietal, and occipital electrodes. In addition, there were a few localized increases in coarse scale MSE (36-40 ms windows) towards the middle/end of the session in central, centro-parietal, and temporo-parietal electrodes.

The second LV ($p = .034$) identified a difference between the beginning (Segments 2, 3, 4) and the end of the session (Segments 9, 10). This pattern revealed fine-scale MSE (2-6 ms windows) increased towards the end of the session in right temporo-parietal, parietal, and occipito-parietal electrodes, and coarse scale MSE (30-40 ms windows) increased towards the end of the session in left central and temporal electrodes, and right fronto-central and centro-parietal electrodes. There were a few very localized decreases in fine to medium scale MSE (16-20 ms windows) in centro-parietal electrodes.

Figure 8*Within Session MSE Results for Session 1*

Note. Top bar at each site represents LV 1, bottom bar represents LV 2. Bar colour indicates direction of effect, with red indicating decreases in MSE, green indicating increases in MSE, and grey indicating no reliable effect. Plot in the bottom left indicates the differences in MSE in LV 1 were found between the beginning versus middle/end of the session. Plot in the bottom right indicates the differences in MSE in LV 2 were found between the beginning versus end of the session. Error bars represent 95% confidence intervals.

Discussion

The purpose of the present study was to investigate neural alterations associated with behavioural changes (Keuleers et al., 2010, 2012) that have been reported with learning on a visual word recognition task, the LDT. As such, we explored neuroplasticity involved in LDT learning, through a replication of the BLP (Keuleers et al., 2012), in which participants completed 16 hours of LDT learning. We measured EEG on three occasions (at the beginning of learning, just prior to midway through learning, and at the end of learning) and obtained two measures of neural response: ERPs and signal complexity. In line with our expectations, we found evidence of behavioural change through decreases in LDT response time across learning. We also found evidence of neural change across learning, through alterations in ERPs (N170, P200, N400, LPC), as well as alterations in MSE.

In the behavioural analyses, we examined changes in response time for words and nonwords separately, in order to make direct comparisons to the response time changes found in the BLP. We found that response time decreased across the three EEG sessions, suggesting that LDT learning improved the efficiency of visual word recognition. While our findings are generally consistent with those of the BLP (Keuleers et al., 2012), we did observe a slightly

different pattern of response time changes with learning. In our results, for the nonword trials we found a significant decrease from the first to second session, as well as from the first to third session, with response time plateauing between the second and third sessions. This is in line with the response time changes found in the BLP. For the word trials, we found a significant decrease in response time from the first to third EEG sessions, but not between the first and second EEG sessions, perhaps suggesting that, as assessed on word trials, changes to visual word recognition happened slightly later in our study than in the BLP. For the analysis of response accuracy, we found very similar results to those of the BLP, such that response accuracy was higher for nonwords than for words throughout the experiment, and for each stimulus type, response accuracy remained relatively constant throughout the experiment. The only difference was that in our experiment, response accuracy to words was slightly higher than for words in the BLP. This may partly be due to our restricted inclusion of stimuli that had response accuracy of 10% or higher in the BLP, thus removing more difficult stimuli that would have reduced overall response accuracy.

Our results suggest that neural alterations also occurred during learning on the LDT. The task PLS analyses on the ERPs revealed that neural changes occurred early in learning during the first EEG session and stabilized thereafter. This analysis highlighted changes in four ERP components: the N170, N400, and LPC, which aligned with our expectations, and additionally the P200. A more detailed view of early learning effects within the first EEG session revealed two patterns of change in the ERPs: the first indicated a change in activity from the beginning to the end of the session, which highlighted effects in the N170, P200, N400, and LPC, and the second indicated a change in LPC activity in the middle of the session compared to the beginning and end. The learning-related effects for each component will be described in more detail below.

Taken together, these patterns of change within and across sessions suggest that neural activity, as measured by ERPs, changed during the first part of learning on the LDT (i.e., during the first session), and these changes remained relatively stable for the remainder of learning.

The N170 increased with LDT learning, becoming more negative over time in bilateral occipito-parietal electrodes. This increase occurred early in learning within the first session, but remained stable between the second and third sessions. Previous research has associated the N170 with visual orthographic processing, based on findings that greater N170 amplitudes are produced for orthographic compared to nonorthographic stimuli (Bentin et al., 1999; Maurer et al., 2005; Simon et al., 2004). However, one study found that N170 amplitude was increased in a task condition focused on identifying words (the LDT) compared to a task condition focused on identifying a specific letter in a presented word, which suggests the N170 may also show sensitivity for lexical word properties, rather than just visual orthographic processing (Proverbio & Adorni, 2009). In addition, from a behavioural perspective, Hargreaves et al. (2012) found a smaller semantic (concreteness) effect in LDT for Scrabble experts compared to nonexperts, and inferred that orthographic processing may be more primary to making lexical decisions for Scrabble experts. Similarly, our finding that N170 amplitude increased early in learning may reflect a learning-related change to greater reliance on visual orthographic processing when making lexical decisions, or perhaps greater reliance on lexical properties of words in general.

The task PLS analysis also revealed alterations to the P200 with LDT learning. In bilateral fronto-central electrodes, the P200 increased within the first session, as well as across the three sessions, becoming more positive later in learning. Originally, we did not expect this component to show learning-related change with LDT learning, as the P200 is generally not examined in this context. Rather, it is typically considered in the context of attentional

processing, where increases in attention are associated with decreased P200 amplitudes in various task conditions (Crowley & Colrain, 2004; Lee et al., 2019; Yuan et al., 2007, 2011). In relation to language, the P200 is related to sublexical processing, such as syllable parsing. Several studies found that frontal P200 amplitude was inversely related to the degree of supposed lexical activation that stems from early sublexical/syllable processing (Barber et al., 2004; Carreiras et al., 2005; Chetail et al., 2012; Comesaña et al., 2012; Lee et al., 2019). For example, words with higher frequency initial syllables, which are associated with weaker P200 amplitudes than low frequency initial syllables, are assumed to activate more items in the lexicon during word recognition, suggesting that reduced P200 amplitude is associated with facilitated syllable parsing and thus lexical activation (Barber et al., 2004; Chetail et al., 2012). In a study where the colour boundary of a multicoloured word was mismatched from the syllable boundary, greater P200 amplitude was found, which the authors suggested hindered syllable parsing and lexical activation (Carreiras et al., 2005). Based on previous attentional research showing that decreased P200 amplitudes are associated with increased attention (Crowley & Colrain, 2004; Lee et al., 2019; Yuan et al., 2007, 2011), the increased P200 amplitudes observed in the current study, both within the first session and across all three sessions, are consistent with an interpretation where the requirement for attentional processing decreases over time as learning occurs on the LDT. Alternatively, drawing from evidence of associated sublexical processing P200 effects (Barber et al., 2004; Carreiras et al., 2005; Chetail et al., 2012), our results may indicate a change in reliance on sublexical processing during visual word recognition. However, due to the uncertainty surrounding interpretation of this effect, more work needs to be done to understand the P200 effect observed in our study with regard to LDT learning.

The analyses also revealed decreased N400 effects with learning. N400 amplitude became less negative with learning, both within the first session and from the first to second session in bilateral frontal and fronto-central electrodes. Although the N400 has traditionally been related to semantic incongruity, with effects found in centro-parietal electrodes (e.g., Kutas & Hillyard, 1980), N400 effects also have been found in frontal electrodes with single word presentations and relating to a variety of conditions (e.g., Barber et al., 2013; Haro et al., 2017; McCarthy & Nobre, 1993; Simon et al., 2004). In fact, N400 effects occur with various types of stimuli and in various topographical distributions, so there is still uncertainty surrounding interpretation of the N400. As it seems that the processing of meaning is central to N400 effects across contexts, one hypothesis is that N400 effects reflect the ease of processing stimulus meaning, with a decrease in amplitude reflecting facilitated semantic processing (Kutas & Federmeier, 2011). This possibility is in line with previous findings examining altered semantic processing with LDT practice and lexical expertise. For example, in a reanalysis of the BLP dataset, previous work found that effects of certain semantic richness variables (e.g., imageability) decreased across LDT blocks (Hargreaves & Pexman, 2012), and, as mentioned, reduced effects of semantics on lexical decision times were found in Scrabble experts compared to controls (Hargreaves et al., 2012). One study also found reduced N400 amplitudes for processing of onomatopoeic words compared to control words, which was interpreted to reflect increased ease of lexical access (Peeters, 2016). Based on these previous findings, the N400 effects in our study may suggest that LDT learning is associated with reduced semantic processing or facilitated lexical access.

The LPC showed a less consistent pattern of change in the different analyses conducted. Across the three sessions in bilateral centro-parietal and parietal electrodes, LPC amplitude

decreased from the first to the second session, and stayed consistent thereafter. Within the first session, however, two different patterns of change emerged. In the electrodes highlighted in the across session analysis, LPC amplitude increased over time within Session 1 (LV 1; see Figure 6a). In left central and centro-parietal electrodes, the LPC amplitude initially decreased, and then increased toward the end of the session (LV 2; see Figure 6b). Thus, overall the results suggest that LPC amplitude increased during the first learning session, but this increase was more pronounced in bilateral centro-parietal and parietal electrodes than in left central electrodes. Previous research has linked the LPC to cognitive resource allocation and stimulus evaluation (Ito & Cacioppo, 2000; Yao & Wang, 2014), with reduced amplitudes observed in task conditions that require fewer attentional or cognitive resources, whereas increased amplitudes are observed in conditions that require greater attentional or cognitive resources (Herring et al., 2011; Ito & Cacioppo, 2000; West & Holcomb, 2000). Because the LPC amplitude increased within the first session, the previous inferences regarding LPC effects suggest that greater reliance on attentional and/or cognitive resources was needed during initial learning, when the LDT task was novel and performance was less skilled and effortful. However, as LPC amplitude decreased for the second and third sessions, our results are consistent with the interpretation that fewer attentional and/or cognitive resources were required later on, as learning had occurred, and performance became more skilled and efficient.

Overall, our ERP findings highlight that neural changes accompany the shift from novel task performance that is less skilled and effortful, to learned performance that is more skilled and efficient. Regarding the cognitive processes related to LDT performance, our findings suggest a shift towards decreased reliance on attentional processing and cognitive resource allocation. In terms of the lexical processing involved in visual word recognition, and borrowing from the

inference made by Hargreaves et al. (2012), the increased N170 amplitude found later in learning could indicate a learning-related shift to greater reliance on orthographic processing while making lexical decisions and less reliance on semantic processing, supported by our finding of reduced N400 amplitude later in learning.

In addition to finding ERP changes with LDT learning, our task PLS analyses also revealed learning-related changes with our measure of complexity, MSE. Over the three sessions MSE mainly decreased across the scalp from the first session to the latter two sessions, except for a few localized MSE increases, suggesting that MSE began to change during the first session. Across the three sessions, fine and coarse scale decreases occurred in bilateral frontal and central electrodes, as well as left posterior electrodes, while coarse scale increases occurred in right posterior electrodes. Within the first session we identified two patterns of change for MSE, which, when taken together, indicate mostly decreases in MSE over time, with a few localized increases. More specifically, the first pattern of change (LV 1) indicated widespread decreases in MSE across the scalp within the first session, with specific coarse scale increases in mainly right centro- and temporo-parietal electrodes. The second pattern of change (LV 2) indicated fewer changes in MSE overall compared to LV 1, but among these changes were more MSE increases than decreases within the first session, such that specific decreases were located in centro-parietal and parietal electrodes, whereas fine scale increases were found in right posterior electrodes, and coarse scale increases were found bilaterally in central electrodes.

Given the widespread MSE decrease observed from the first to second and third sessions, as well as the decreases within the first session, it appears that while performance was initially less skilled and effortful, a change occurred such that processing became more honed and optimized, and performance more automatic. Once this learning-related change occurred, this

level of performance was maintained. As suggested by Heisz et al. (2012), although the processes involved may not be exactly the same as repetition suppression, these MSE decreases could be explained similarly to theories of repetition suppression (Desimone, 1996; Grill-Spector & Malach, 2001; Henson & Rugg, 2003; Miller & Desimone, 1994; Wiggs & Martin, 1998), such that neural response became simplified in some way (Burles et al., 2019), thereby optimizing processing and making visual word recognition processes more automatic. Along with these decreases, there were also specific, localized increases mainly in right posterior electrodes, which suggests an enrichment of processing was occurring to a small degree. Using the interpretation that MSE increases may reflect greater flexibility with regard to processing or response options available (e.g., Burles et al., 2019; Heisz et al., 2012), the specific increases observed in our results may indicate that in addition to the widespread streamlining of processing, with LDT learning there appears to also be an enrichment of processing through greater processing flexibility.

Limitations

Taken together, our results indicate evidence of both behavioural and neural change with learning on a visual word recognition task. Of course, the study is not without limitations. In our experiment, response time was not collected during the LDT blocks completed out of the lab as we judged that differences in internet connection speeds would have affected the accuracy of response time measurements. Though the response time measurements taken during the in-lab EEG sessions provided evidence of an increase in efficiency through the decreased LDT response time observed across the sessions, more could be learned from examining the pattern of response time change across all blocks in the experiment. In addition, we had a fairly small sample size in comparison to many behavioural studies, such as the BLP (Keuleers et al., 2012),

but we were able to replicate the behavioural results of the BLP with our sample. If the behavioural effects are to become a main focus in future studies, a bigger sample size may be beneficial, and may be able to confirm whether the effects found in this study are similar to those obtained with a larger sample. However, our sample size is consistent with other ERP studies (Luck, 2014a), and due to the large number of trials in our analyses (approximately 1,000 trials per participant, per EEG session), and in addition to the within-subjects design of our experiment, this helps to ensure adequate statistical power of our design (Luck, 2014b) and adds to the robustness of the effects found in the current study.

Conclusion

Despite evidence of stability for the visual word recognition system throughout adulthood (e.g., Cohen-Shikora & Balota, 2016), the current study replicated previous findings of performance alterations (Keuleers et al., 2010, 2012) and extended these by showing that neural change also occurs with learning on a visual word recognition task. Specifically, our findings suggest there is considerable flexibility involved in the visual word recognition system, with changes in orthographic and semantic processing, attention, and cognitive resource allocation associated with more efficient visual word recognition. In addition, the finding of decreased brain signal complexity suggests that with learning, processing becomes more automatic, honed, and optimized. As the neural changes occurred rapidly after task onset, this suggests a flexible and dynamic visual word recognition system, with a capacity to increase the efficiency of task performance.

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