Discovering the brain stages of lexical decision: Behavioral effects originate from a single neural decision process

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1. Introduction

Language encompasses our daily life — whether it is a simple chat with family or friends, a more formal presentation at work, or reading the newspaper. One aspect involved in language processing is recognizing words from a sequence of phonemes or a string of letters. A common paradigm for studying word recognition is a lexical decision task (LDT; Meyer & Schvaneveldt, 1971). In this paradigm, participants are asked to indicate whether a sequence of letters presented on the screen is an existing word or a nonword. Although behavioral differences between types of words/nonwords have been robustly detected in LDT, there is an ongoing discussion about the exact cognitive processes that underlie the word identification process in this task. To obtain data-driven evidence on the underlying processes, we recorded electroencephalographic (EEG) data and applied a novel machine-learning method, hidden semi-Markov model multivariate pattern analysis (HsMM-MVPA) in the current study, participants performed an LDT in which we varied the frequency of words (high, low frequency) and “wordlikeness” of non-words (pseudowords, random non-words). The results revealed that models with six processing stages accounted best for the data in all conditions. While most stages were shared, Stage 5 differed between conditions. Together, these results indicate that the differences in word frequency and lexicality effects are driven by a single cognitive processing stage. Based on its latency and topology, we interpret this stage as a Decision process during which participants discriminate between words and nonwords using activated lexical information.

1.1. Lexical decision task

One important phenomenon that has been observed in LD is the word frequency effect — words that occur more frequently in the lexicon (high frequency words; HF) are on average recognized more quickly than less frequent words (low frequency words; LF). Yet, there is an ongoing discussion about the exact point in the trial at which the differences between conditions occur and infer which cognitive processes they are associated with.

In the remainder of the introduction, we will present the main findings from the lexical-decision literature and describe the rationale for HsMM-MVPA analysis applied to EEG data.

Keywords:
Lexical decision
Electroencephalography
Event-related potentials
Machine learning
Multivariate pattern analysis
Hidden semi-Markov Models

ARTICLE INFO

Abstract

Lexical decision (LD) – judging whether a sequence of letters constitutes a word – has been widely investigated. In a typical lexical decision task (LDT), participants are asked to respond whether a sequence of letters is an actual word or a nonword. Although behavioral differences between types of words/nonwords have been robustly detected in LDT, there is an ongoing discussion about the exact cognitive processes that underlie the word identification process in this task. To obtain data-driven evidence on the underlying processes, we recorded electroencephalographic (EEG) data and applied a novel machine-learning method, hidden semi-Markov model multivariate pattern analysis (HsMM-MVPA). In the current study, participants performed an LDT in which we varied the frequency of words (high, low frequency) and “wordlikeness” of non-words (pseudowords, random non-words). The results revealed that models with six processing stages accounted best for the data in all conditions. While most stages were shared, Stage 5 differed between conditions. Together, these results indicate that the differences in word frequency and lexicality effects are driven by a single cognitive processing stage. Based on its latency and topology, we interpret this stage as a Decision process during which participants discriminate between words and nonwords using activated lexical information.

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In this research, we aim to obtain evidence on the underlying cognitive processes of LDT. To that end, we will apply a novel machine-learning algorithm: hidden semi-Markov model multivariate pattern analysis (HsMM-MVPA; Anderson, Zhang, Borst, & Walsh, 2016). This is a data-driven method that can discover processing stages from electroencephalographic (EEG) data. Using HsMM-MVPA, one can detect how many cognitive stages drive performance, and characterize these stages based on their latency and topology. Unlike two common methods previously used to analyze LDT – behavioral analyses that use a single measure per trial and event-related potentials (ERPs) that use averages of the EEG signal over trials and participants – HsMM-MVPA takes all data of the experiment into account simultaneously. As a result, HsMM-MVPA allows finding the exact point in the trial at which the differences between conditions occur and infer which cognitive processes they are associated with.

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frequent words (low frequency words; LF; e.g., Balota & Chumbley, 1984; Fiez, Balota, Raichle, & Peterson, 1999; Scarborough, Cortese, & Scarborough, 1977). Another robust phenomenon is the nonword lexicality effect that reflects that “wordlike” nonwords (pseudowords) are recognized more slowly than random nonwords (Fiez et al., 1999; Ratcliff et al., 2004; Stone & Van Orden, 1993; Wagenmakers et al., 2004).

Traditionally, the observed differences between HF and LF words were attributed to lexical access, that is, the process of retrieving the word from the mental lexicon (Becker, 1980; Donkin & Heathcote, 2009; Morton, 1969; Paap, Newsome, McDonald, & Schvaneveldt, 1982; Perea, Rosa, & Gómez, 2002; Schilling et al., 1998). In these models, the assumption was made that various word identification tasks share the same underlying process, lexical access, with a minor role for decision-related processes (Andrews & Heathcote, 2001). For example, in the conventional logogen model (Morton, 1969), the word frequency effect is due to a higher resting activation level of lexical units in HF words than in LF words (for an overview of models of lexical access, see Andrews, 1989). Paap et al. (1982) suggested a similar process for pseudowords, where words that are orthographically similar to the pseudowords are being retrieved from the lexicon. This explains why pseudowords are often mistaken with real words and are characterized by lower accuracy than nonwords (Grainger, Bouttevin, Truc, Bastien, & Ziegler, 2003).

In reaction to the finding that the word frequency effect was larger in the LDT than in other word recognition tasks, an alternative view was proposed (Balota & Chumbley, 1984; Besner, 1983; McCann, Besner, & Daveelaar, 1988; Ratcliff et al., 2004; Stone & Van Orden, 1993; Wagenmakers, Ratcliff, Gomez, & McKoon, 2008). For example, Balota and Chumbley (1984) suggested that the differences in the LDT are driven by task-specific decisional or familiarity processes, rather than pure lexical access. In this frame, Ratcliff and colleagues (2004) explained the effects of word frequency and type of nonwords as altering the “amount and kind of information … that drives the decision process and nothing more” (p. 20). Continuing this idea, Wagenmakers and colleagues (2008) showed that strategic factors also influence performance on the LDT by manipulating speed versus accuracy instructions.

Although mean reaction time (RTs) measures have been traditionally used to investigate frequency and lexicality effects, more sophisticated methodologies are needed to identify the processes underlying LDT. Recent studies demonstrated that not only the average RT measure is indicative of these effects, but the shape of the whole RT distribution (Andrews & Heathcote, 2001; Balota & Spieler, 1999; Perea et al., 2005; Tillman, Oth, van Ravenzwaaij, & Heathcote, 2017). An alternative approach is the signal-to-respond paradigm where accuracy rather than speed of response was used as the variable of interest (Hintzman & Curran, 1997; Wagenmakers et al., 2004; Zeelenberg, Wagenmakers, & Shiffrin, 2004). However, even these more advanced behavioral methods could not clearly identify underlying cognitive processes. Thus, for example, Balota and Spieler (1999) found that the word frequency and lexicality had a different effect on RT distribution for naming and LDT tasks. Although these differences were interpreted as the presence of the familiarity processes in LDT, there was no clear support for this.

With the advent of neuroimaging, researchers turned from behavioral measures to functional imaging. In this frame, functional Magnetic Resonance Imaging (fMRI) was used to identify the brain networks underlying the word recognition process in LDT. In a recent study on LDT and wordlike reading, common reading-related regions including ventral occipito-temporal cortex and inferior frontal gyrus (IFG) were found (Wang et al., 2015). Additionally, task-specific activations in precentral gyrus and insula were detected in LDT, linked to motor preparation and error monitoring, respectively (Taylor, Stern, & Gehrig, 2007). In another study on LDT and reading aloud, it was found that both tasks shared a wide variety of common brain areas associated with orthographic, semantic and phonological processing (Carreiras, Mechelli, Estévez, & Price, 2007). Moreover, in LDT, task-specific activations were reported at bilateral postcentral gyri, supplementary motor area, and right cerebellum linked to decision-making and motor planning. Overall, this suggests that besides common reading processes, there are task-specific cognitive processes involved in LDT associated with decision making.

Due to its advantage of very high temporal resolution, EEG has been applied to LDT to investigate the temporal order of the different underlying processes. Because it is difficult to extract information about cognitive processing from raw EEG data, event-related potentials (ERPs), averages of the signal locked to a particular temporal event, were calculated from LDT-EEG data. One of the most robust findings was the N400 component, which negative amplitude was seen as the inverse of word frequency (Barber & Kutas, 2007; Barber, Vergara, & Carreiras, 2004; Kutas & Federmeier, 2011; Rugg, 1990). This component has also been observed for nonwords lexicality effects with pseudowords eliciting more negative amplitudes than words (Barber, Otten, Kousta, & Vigliocco, 2013; Carreiras, Vergara, & Barber, 2005; Holcomb, Grainger, & O’Rourke, 2002; Lau, Phillips, & Poeppel, 2008) and random non-words (Holcomb & Neville, 1990; Nobre & McCarthy, 1998).

Another ERP component that was found to vary between words/nonwords is a positively going P600, also referred to as the Late Positive Component (LPC). It has been found that words are characterized by a higher amplitude P600 as compared to pseudowords (Bermúdez-Margaretto, Beltrán, Domínguez, & Cueto, 2015; Curran, 1999; Proverbio & Adorni, 2008). In studies where a task different than LDT was used, P600 was found to be associated with word frequency (Rugg, 1990; Young & Rugg, 1992). Another interesting finding was that not only the amplitude was associated with these effects but also the latency: the P600 was found to be longer for LF than HF words (Polich & Donchin, 1988).1

Although amplitude effects of these components are well established, the temporal locations are less well defined. For example, for the negative-going N400, not only the reported interval is large (>200 ms) but also different between studies: 250–450 ms (Barber et al., 2013); 300–500 ms (Rugg, 1990); 350–500 ms (Barber et al., 2004); 250–500 ms (Nobre & McCarthy, 1994); 300–650 ms (Carreiras, Vergara, & Perea, 2007). For the P600, similar timing differences were observed: 400–700 ms (Curran, 1999); 500–618 ms (Bermúdez-Margaretto et al., 2015); 600–800 ms (Proverbio & Adorni, 2008); 500–800 ms (Young & Rugg, 1992). An important reason for this is the trial-by-trial variability in these peaks, which is more pronounced further from fixed time points (Borst & Anderson, in press; Walsh, Gunzelmann, & Anderson, 2017; Zhang, Walsh, & Anderson, 2018). The more variable a peak is between trials, the wider the component will be when calculating ERPs.

Overall, this makes it difficult to conclude at what particular moments in time differences between types of words and nonwords originate, and consequently, what the driving cognitive process is.

1.2. Hs-MM-MVPA analysis for discovering stages in EEG

Despite the fact that the traditional ERP approach has been instrumental in quantifying the differences in the word recognition process across words and nonwords, it has been limited in identifying the exact temporal locations where different stimuli elicit different brain signatures. If we could use the high temporal resolution of EEG data and precisely identify the timing of these peaks on each trial, then we could address at which point in the trial the differences between various types of words and nonwords arise. These differences could be further explored and associated with the underlying cognitive processes. Here, we will use a novel machine learning algorithm, Hs-MM-MVPA, that uses the
EEG data to detect peaks on a trial-by-trial basis. HsMM-MVPA is a method that allows parsing neural recordings of a cognitive task into different stages that are assumed to represent different, sequential processes (Anderson et al., 2016; Borst & Anderson, in press). To find these stages, Hidden semi-Markov models (HsMMs; Yu, 2010) were combined with multivariate pattern analysis. HsMMs are an extension of standard Hidden Markov Models (HMM; Rabiner, 1989) that allow for variable-duration stages. The onset of each stage is defined as a multivariate pattern across the EEG electrodes (when averaged, parts of these patterns form traditional ERPs). This HsMM-MVPA method has been successfully applied to a range of cognitive tasks including associative memory recognition, arithmetic retrieval, and classical short-term memory tasks (Anderson et al., 2018, 2016; Portoles, Borst, & van Vugt, 2018; van Maanen, Portoles, & Borst, 2021; Walsh et al., 2017; Zhang, Borst, Kass, & Anderson, 2017; Zhang, van Vugt, Borst, & Anderson, 2018; Zhang, Walsh, et al., 2018). In a recent validation study, it was found that HsMM-MVPA allows for zooming into processes identified with RT-based methods by finding a range of corresponding cognitive stages (Berberyan, van Maanen, van Rijn, & Borst, 2021).

The rationale for HSMM-MVPA analysis is the assumption that a cognitive event (i.e., the trigger for a new stage) is accompanied by a peak in the activity in different brain regions. This assumption is in line with two competing theories of ERP generation: the classical theory (Schroeder et al., 1995; Shah et al., 2004) and the synchronized oscillations theory (Makeig et al., 2002), which both assume a peak at the onset of a significant cognitive event. Consistent with this idea, we search for a multivariate peak in activation (a bump) to identify a new cognitive stage. Each bump marks the onset of a new processing stage and is followed by ongoing EEG oscillations that are referred to as a flat. There are multiple cognitive events in a task and, thus, multiple stages. A stage in HSMM-MVPA analysis is viewed as a combination of a bump and a flat, except for the first stage, which starts with stimulus onset and ends at the first bump.

In HSMM-MVPA analysis, an average model is created for all participants and trials. The underlying idea is that participants go through the same cognitive processes, and thus bumps, on each trial. However, as the duration of these processes can vary over participants and between trials, the flats between bumps have variable durations which are modelled as gamma distributions. This is illustrated in Fig. 1, where the red arrows indicate the origin of the second bump, and the blue arrows origins of the gamma distribution describing Stage 4. The method first integrates the data of all participants and trials to define the optimal bumps and gamma distributions that account for the EEG data, and as a result, yields the most probable temporal location of each bump on each trial – allowing for a more detailed analysis of these bumps than is possible with traditional ERPs.

To summarize, in the current EEG study, we aimed to identify the cognitive stages that underlie the LD process and to determine which stages drive the difference between HF, LF, pseudowords, and non-words. To compare our results with the existing literature, we first performed standard behavioral and ERP analyses. Next, we applied the HsMM-MVPA analysis to discover the underlying processing stages. Finally, we calculated bump-related potentials (BRPs) – an extension of classical ERP analysis – by aligning EEG data to the temporal onsets of these stages (Borst & Anderson, in press).

2. Methods

2.1. Participants

Twenty-nine volunteers, students of the University of Groningen, performed the LDT. Three participants were excluded from the analysis: one due to recording problems and two – due to excessive noise in the EEG data. The final set consisted of twenty-six participants (11 females, age range 18–35 years old, mean age = 22.5, SD = 3.2). For their participation, they received a compensation of 8 euros.

All participants were right-handed, had no history of neurological disorders and were Dutch native speakers. Before the experiment, all participants gave written informed consent in accordance with the Declaration of Helsinki. The experimental procedures were approved by the Research Ethics Review Committee (CETO) of the Faculty of Arts at the University of Groningen (reference number 64329605).

2.2. Task

In the experiment, participants were asked to respond whether a combination of letters presented on the screen was an actual Dutch word or not. To respond, participants pressed the corresponding button on the keyboard (‘n’ or ‘m’) with their right hand. If the response was incorrect they received feedback. We varied the natural frequency of the words (HF and LF) and the ‘wordlikeness’ of non-words (pseudowords and random letter strings).
2.3. Materials

To ensure that our results reflect standard LD effects, we based our stimuli on a pre-existing dataset. We used items from the Dutch Lexicon Project (DLP; Keuleers, Diepenaele, & Brysbaert, 2010) that included 14,000 words and 14,000 nonwords. From these, we first selected items with 4–8 characters that had at least 85% accuracy. For the HF condition, we then selected items with a CELEX\textsuperscript{2} frequency (Baayen, Piepenbrock, & van Rijn, 1993) higher than 1000 (mean = 7352.10, SD = 22693.64, n = 1702). For the LF condition, we selected words with a CELEX frequency higher than 3 and lower than 25 (mean = 12.81, SD = 6.17, n = 506). For the Pseudoword condition, we selected nonwords that had a corresponding HF item with a maximum edit distance of 2 and consisted of the same number of characters. For the Random letter strings condition, we created new items by randomly shuffling characters of the LF items and making sure that the new strings did not accidentally form a word. Finally, for each participant, we randomly selected 240 items for each condition and 8 practice items.

2.4. Procedure

Participants were seated in front of a 21.5-inch screen. The experiment was implemented in OpenSesame (Mathôt, Schröij, & Theeuwes, 2012) using the experiment back-end. The experiment consisted of 960 trials presented in four blocks. Each of these blocks contained 240 trials, 60 trials per condition. A practice session of 8 trials preceded the main experimental session. The main experimental part took on average 30–40 min. The entire duration of the experiment including instructions and EEG setup was one hour.

Each trial started with a fixation dot for a random duration between 400 and 600 ms. Next, the stimulus (word/non-word) was presented in 20-points font size. The participants were asked to respond by pressing the button on the keyboard - ‘n’ for words and ‘m’ for non-words. If participants responded incorrectly or did not respond during a specified timeout (2000 ms), the feedback ‘incorrect’ was presented for 2000 ms.

2.5. EEG recording

EEG was acquired from 32 positions using active Ag-AgCl electrodes (Biosemi Active Two system). Data was recorded with a sampling rate of 512 Hz. The electrodes were placed using the international 10–20 system layout. Two channels – Common Mode Sense (CMS) and Driven Right Leg (DRL) – were used as “ground”. Four additional electrodes (two vertical and two horizontal) were used to measure eye movements. For most of the participants, scalp impedance of the electrodes was kept at <20 kΩ, while for six participants it was kept at <30 kΩ.

2.6. Behavioral analysis

Practice trials were excluded for both accuracy and reaction times (RT) analyses. Additionally, for the RT analysis, we excluded all incorrect responses. For each condition and each participant, we then removed trials that deviated more than 3 standard deviations from the mean RTs (1.76% of the trials). This form of outlier rejection was in line with previous HsMM-MVPA studies (e.g., Anderson et al., 2016).

Differences in accuracy and RTs were evaluated with linear mixed-effects models (LMEs; Bates & DeBry, 2004) as implemented in R. LMEs are extensions of linear regression models that allow to flexibly combine fixed and random effects. We obtained p-values for fixed effects, using Satterthwaite’s method (Kuznetsova, Brockhoff, & Christensen, 2017). To obtain the random effects structure that could account best for the data, we fitted various models with random effects and compared the goodness-of-fit by means of likelihood-ratio tests. In this way, we identified the maximum random-effects structure that was supported by the data (Bates, Kliegl, Vasishth, & Baeyen, 2015).

2.7. EEG preprocessing

EEG preprocessing was conducted with the open source EEGLAB toolbox (Delorme & Makeig, 2004) and custom-made scripts in MATLAB. Data was first referenced to the average of the mastoids. Next, a high-pass filter of 0.5 Hz and a low-pass filter of 40 Hz were applied. To detect artifacts in the data manual artifact rejection was performed. On average 5.35% of data was removed during manual artifact rejection. For ten participants, on average 1.5 noisy channels were detected and removed. Next, the data was decomposed with independent component analysis (ICA) using the infomax algorithm runica in EEGLAB. For all participants, one or two components containing eye blinks and muscle movements were identified and subtracted. Finally, the previously removed channels were interpolated with spherical spline interpolation.

2.8. ERP analysis

For ERP analysis, the ‘outliers’ rejection was consistent with the behavioral analysis pipeline (for details, see the 2.6. Behavioral analysis section). In addition, incomplete trials that appeared due to visual artifact rejection in the selected time windows were inspected and removed. Baseline normalization (400 ms preceding the stimulus presentation) was applied to remove slow drifts in the signal. The data from the following time intervals was selected: 200 ms before the stimulus and 600 ms after, 600 ms before the response and 200 ms after, for stimulus-locked and response-locked ERPs, respectively. Grand average event-related potential waveforms elicited by the four conditions were computed for all channels and visually inspected.

To statistically compare the observed differences between conditions, a cluster-based random permutation analysis was performed (Mars & Oostenveld, 2007) in Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). This analysis allows dealing with multiple comparison problems (MCP) and, thus, controlling for type 1 error (“false positive”). The general procedure is as follows: (1) for every sample, the difference between two conditions is calculated using a t-test, (2) clusters are formed based on the neighborhood, and the cluster statistic is calculated as the sum of the corresponding t-values, (3) the data is randomly divided into two conditions many times, and cluster statistics are calculated from that, (4) the proportion of the values from random partitions that exceeded the observed statistic is computed, resulting in a p-value (Monte Carlo approximation).

Because of the within-subject design, the data between conditions was compared by means of a paired t-test. Next, a cluster-level statistic was calculated as the sum of temporally-adjacent t-values that exceeded a p-threshold of 0.05. The data was randomly partitioned into two conditions 1000 times, and the histogram of cluster-level statistics was constructed. Next, the resulting p-value was calculated. The critical alpha level was specified as 0.05 meaning that if the p-value was smaller than 0.05, we concluded that the compared conditions were significantly different. The analysis was performed for all channels and conditions.

2.9. Preprocessing for HsMM-MVPA analysis

The trial selection for the HsMM-MVPA analysis was identical to the ERP analysis. For this analysis, the data from each individual trial was selected from stimulus presentation to response execution. Next, preprocessing specific to HsMM-MVPA analysis was performed (Anderson et al., 2016).

First, the data was downsampled to 100 Hz for computational efficiency, followed by a principal component analysis (PCA). First, the variance of each participant was scaled to the mean variance in the data to ensure that the data from all participants contributed equally to the

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2 Raw frequency that is specified by CELEX database
results. Next, the covariance matrix was computed for each trial, and PCA analysis was performed on the average covariance matrices (Cohen, 2019; Portoles et al., 2018). Following previous HsMM-MVPA analyses, 10 PC components, which explained 90.5% variance of the data, were used in the analysis. Finally, these PC components were z-scored per trial.

2.10. HsMM-MVPA application to EEG

The HsMM-MVPA analysis was applied to the EEG data to discover the processing stages underlying task performance. As described above (1.2. HsMM-MVPA analysis for discovering stages in EEG) a cognitive stage consists of a “bump” that is followed by a “flat”. Because bumps characterize cognitive processes that are assumed to be the same across all subjects, they have fixed topologies. On the other hand, the duration of these processes varies over trials, which is why the flats are described with gamma distributions.

In HsMM-MVPA analysis, several preliminary assumptions are made regarding bumps and flats. The width of the bumps is defined as 50 ms. Although the ‘real’ bumps could be narrower or wider than that, analyses on synthetic data revealed that the duration of 50 ms allows for robustly detecting bumps with a width of 30–110 ms (Anderson et al., 2016). The flats follow gamma distributions with a shape parameter of 2. While the shape parameter is fixed, the scale parameter of the gamma distribution is estimated. Bumps mark the transition to a new stage and thus initiate all stages except for the first stage that begins with stimulus presentation. Therefore, the placement of n bumps in a trial results in n + 1 flats.

HsMM-MVPA analysis is performed on all data simultaneously, and yields estimated bump locations per trial. The HsMM-MVPA analysis searches for the locations of the bumps, which are defined by a multivariate amplitude pattern. For maximum likelihood estimation, the standard expectation–maximization (EM) algorithm was used which is especially powerful when dealing with latent variables (Zhang, Brady, & Smith, 2001). As the expectation of EM, “E-Step”, we computed estimates for bumps (i.e., the amplitude) and flats (i.e., the scale parameter of the gamma distribution). As the maximization of EM, “M–Step”, we computed the maximum likelihood for these estimates. The steps repeat until the algorithm converges. This procedure results in estimates for the amplitude of the bumps, the scale parameters of the gamma distributions, and the probability of the location of each bump on each trial.

Our analysis started with the identification of good initial estimates for the parameters describing the bumps and gamma distributions, to avoid local maxima during subsequent EM estimations (Berberyen et al., 2021; Zhang, Walsh, et al., 2018). This was done by first fitting an HsMM model with the maximum number of bumps to the data (as bumps cannot overlap, this is the duration of the shortest trial divided by the 50-ms bump width). Next, models were fitted where one of these previously identified bumps was iteratively excluded. From these iterative models, we selected the one with the highest goodness-of-fit (i.e., log-likelihood). The described steps were repeated up to the model with 1 bump. The bump amplitudes and gamma distributions obtained in this way were then used in subsequent HsMM models as the starting parameters.

Next, to obtain the number of bumps that can account best for the data, HsMM models were fitted starting from 1 bump to the maximum number of bumps that fit in the data. Because the log-likelihood of a model typically increases when more bumps are fitted due to the increased flexibility of the model, a leave-one-out cross-validation (LOOCV) procedure was applied. For this aim, we fitted a model to all participants but one and tested the resulting parameters on this participant. The described procedure was repeated for all participants. A more complex model was preferred only if it outperformed a more parsimonious model for a significant number of participants.

2.11. BRP analysis

To extend the classical ERP analysis, we calculated bump-related potentials (BRPs). BRPs were calculated for each problem type by aligning EEG data to the most probable location of a bump on each trial identified with HsMM-MVPA. Next, for averaging purposes, the data was resampled to the average location of the bumps across trials. Finally, the grand average bump-related potential waveforms were calculated per condition. The differences between conditions were subjected to the same cluster-based random permutation analysis as the ERPs (for details, see 2.8. ERP analysis section).

3. Results

3.1. Behavioral results

Average error rates and RTs were computed for each participant and each condition. Next, average values per condition along with within-subject standard errors were calculated (Morey, 2008); these values are shown in Fig. 2. Reaction times were shortest for random non-words, followed by HF words, LF words, and pseudowords. Error rates followed the same pattern. These findings are consistent with the literature (e.g., Fiez et al., 1999; Ratcliff et al., 2004; Schilling et al., 1998; Wagemakers et al., 2008) and the values previously reported for these stimuli (Keuleers et al., 2010).

To evaluate the observed differences statistically, LMEs were constructed. For both RTs and accuracy, a forward fitting procedure was
applied. This revealed that the models with Condition as a fixed effect, Subject and Item as random intercepts and Trial as a random slope explained the most variance. For both accuracy and reaction times, significant differences were found between all conditions. The results are presented in Table 1.

3.2. ERP results

Grand average stimulus-locked ERPs were calculated for each condition. Fig. 3 shows 9 channels across the scalp, stimulus-locked (for response-locked ERPs, see Appendix 1). Significant clusters of condition differences are indicated with horizontal lines. The two main ERP components that are typically reported in LDT, N400 and P600, were

Table 1

|                  | B    | SE   | t     | p     | B    | SE   | z     | p     |
|------------------|------|------|-------|-------|------|------|-------|-------|
| Reference level: HF |      |      |       |       |      |      |       |       |
| Intercept        | 623.04 | 12.80 | 48.66 | <0.001 | 4.53 | 0.12 | 36.87 | <0.001 |
| LF               | 57.98  | 3.60  | 16.09 | <0.001 | -1.26 | 0.13 | -9.57 | <0.001 |
| Pseudo           | 120.16 | 3.35  | 35.83 | <0.001 | -1.58 | 0.12 | -13.47 | <0.001 |
| Random           | -32.72 | 3.55  | -9.21 | <0.001 | 1.04  | 0.18 | 5.74  | <0.001 |
| Reference level: LF |      |      |       |       |      |      |       |       |
| Intercept        | 681.02 | 12.90 | 52.78 | <0.001 | 3.27  | 0.11 | 30.45 | <0.001 |
| Pseudo           | 62.18  | 3.72  | 16.73 | <0.001 | -0.31 | 0.11 | -2.82 | <0.01  |
| Random           | -90.69 | 3.89  | -23.27 | <0.001 | 2.30  | 0.18 | 12.72 | <0.001 |
| Reference level: Pseudo |      |      |       |       |      |      |       |       |
| Intercept        | 743.20 | 12.84 | 57.90 | <0.001 | 2.95  | 0.09 | 31.87 | <0.001 |
| Random           | -152.87 | 3.67  | -41.66 | <0.001 | 2.62  | 0.17 | 15.36 | <0.001 |

Fig. 3. Grand average ERPs for four conditions: HF (high frequency), LF (low frequency), Ps (pseudowords) and Rnd (random non-words) complemented with standard errors (shaded areas). The lines below the grand averages indicate significant clusters of differences between conditions. The location of these lines on the horizontal axis corresponds to the temporal locations of the significant differences. The clusters significant at 0.05 are marked with an asterisk (*) and at 0.01 with a rectangle (□).
found.

Over central, parietal and temporal regions, the N400 was present with LF words eliciting more negative amplitudes than HF words and pseudowords being more negative than words. Our findings are consistent with the body of literature on the N400 linked to word frequency (e.g., Barber et al., 2004; Rugg, 1990). Moreover, the higher amplitude of the N400 was consistently reported for pseudowords as compared to words (e.g., Carreiras et al., 2005; Wang & Yuan, 2008) and to random nonwords (e.g., Coch & Mitra, 2010; Ziegler, Besson, Jacobs, Nazir, & Carr, 1997).

In addition, the positive-going P600 was observed. Most prominent at central and parietal locations, pseudowords elicited lower amplitude in the P600 as compared to random nonwords (Holcomb & Neville, 1990) and words (Ziegler et al., 1997). Additionally, HF words elicited more positive amplitudes in the P600 than LF words. This is in line with findings that the P600 is commonly associated with lexicality (e.g., Bermúdez-Margaretto et al., 2015; Holcomb & Neville, 1990) and, in some cases, with frequency effects (Young & Rugg, 1992).

### 3.3. HsMM-MVPA results

#### 3.3.1. Number of stages in lexical decision

Under the assumption that cognitive stages are shared between the four different conditions: HF, LF, Random and Pseudowords, we started with a general model for all conditions. The results of the leave-one-out-cross-validation are shown as the blue line in Fig. 4. Five bumps – and thus six stages – were found to account best for the data, both in overall log-likelihood and in displaying an improvement over a solution with four bumps for a significant number of participants (19 of 26 participants, \( p = 0.03 \) as indicated by a sign test). In addition – to check whether this result was not due to pooling the data across conditions – we tested separate models for each condition. In all these models, five bumps were found to account best for the data (Table 2). We conclude that a model with five bumps and six stages best describes lexical decision, independent of condition.

#### 3.3.2. Model selection

Initial visualisation of the models (not shown) revealed apparent differences in the duration of Stage 5 between conditions (the flexibility of the gamma distribution allows for this). To test whether the duration of this stage indeed needs to differ between conditions, we constructed two additional models: a model with only the duration of Stage 5 differing between conditions (i.e., each condition has its own gamma distribution for Stage 5) and a model with both Bump 5 and the duration of Stage 5 being different. The results are illustrated in Fig. 4 as the orange-red and the purple dots, respectively. The model where we varied the duration of Stage 5 across conditions clearly provided a better fit for a significant number of participants compared to the general model (25 of 26 participants, \( p < 0.001 \) as indicated by a sign test). The model where we varied both the duration of Stage 5 and Bump 5 had the highest log-likelihood (Fig. 4). Moreover, for a significant number of participants (19 of 26, \( p = 0.03 \)), it outperformed the model where we varied only the duration of Stage 5.

For exploratory purposes, we also constructed models where the durations of other stages and the bumps varied per condition. None of these models outperformed the models above. On this basis, we conclude that a model with Bump 5 and Stage 5 being different across conditions while the other stages are shared, accounts best for the lexical decision process.

#### 3.3.3. The resulting HsMM-MVPA model

The resulting HsMM-MVPA model is illustrated in Fig. 5. While Stages 1–4 and 6 are shared across conditions, Stage 5 is characterized by different durations between conditions, with the overall RT effect clearly originating in this stage. To evaluate these differences statistically, we constructed LMEs in R with the lmerTest package (Kuznetsova et al., 2017). A forward fitting procedure identified that the model with Condition as a fixed effect, Subject as a random intercept and Trial as a random slope explained the most variance. The duration of Stage 5 was different between all conditions (see Table 3 for summary statistics).

In the resulting HsMM-MVPA model, along with the fifth stage, the last bump varied between conditions and was characterized by a prominent parietal positivity. We compared the amplitude of Bump 5 for each channel and condition pair using paired t-tests followed by false discovery rate control across channels (FDR; Benjamini & Hochberg, 1995). Paired t-tests revealed significant differences between the following conditions: Pseudo-HF, Pseudo-LF, Random-HF and Random-Pseudo (see Fig. 6). While the differences between Random-HF and Random-Pseudo were observed only in very few channels, the differences between Pseudo-HF and Pseudo-LF were clustered in the spatial domain, mainly in the left parietal and occipital channels.

### 3.4. BRP results

Grand average BRPs were calculated for each condition and

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**Table 2**

| Type of model | Number of bumps |
|--------------|-----------------|
|              | 2 > 1 | 3 > 2 | 4 > 3 | 5 > 4 | 6 > 5 |
| General model | 23   | 23   | 25   | 19   | 15 |
| HF model     | 25   | 24   | 25   | 23   | 14 |
| LF model     | 25   | 21   | 25   | 24   | 10 |
| Random model | 26   | 25   | 25   | 25   | 18 |
| Pseudo model | 24   | 23   | 26   | 20   | 8 |

**Fig. 4.** The fits of the three models: the general model, a model where the duration of Stage 5 is assumed to differ between conditions, and a model where Bump 5 and the duration of Stage 5 are assumed to differ between conditions. The blue numbers associated with the general model indicate the number of participants for which the model improved as compared to a simpler model with fewer bumps (e.g. model with 2 bumps vs. a model with 1 bump). The values for “Stage 5 different” and “Bump 5 and Stage 5 different” models represent an improved fit as compared to simpler models with the same number of bumps. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
presented for 9 channels across the scalp in Fig. 7. The cluster-based permutation analysis identified clusters of differences that are indicated with horizontal lines below the grand averages. Consistent with the ERP results, most of the differences in the amplitudes were observed in two consecutive ERP components: the N400 and P600. The N400 effect was observed for all conditions with pseudowords eliciting more negative amplitudes than words and random non-words. This component also accounted for frequency effects with more negative amplitudes for LF than HF. As in the ERPs, across central and parietal channels, pseudowords elicited lower amplitudes for P600 than the other conditions. In addition, the P600 component also accounted for frequency effects in some channels, particularly Pz.

The largest difference between ERPs and BRPs is that the latter allows for identifying the exact timings of the peaks for each condition. Most notably, not only the amplitude of the P600 peak was different between conditions but also its temporal location. This was not clear in the ERP results reported above, nor in the response-locked ERPs in the Appendix 1. These differences in the location of the P600 can directly be related to the HsMM-MVPA results: Stage 5 starts at the N400 and ends at the P600, and is clearly the underlying factor in the RT differences between the conditions.

4. Discussion

In the current study, we investigated the brain stages determining performance in lexical decision. While the LDT task has been widely investigated and has yielded robust behavioral and ERP findings, there has been an ongoing debate on the cognitive interpretation of these findings, in particular about the origin of the word frequency and nonword lexicality effects. To pinpoint the origin of these effects, we used a machine learning method that discovers the underlying cognitive stages directly from EEG.

To ensure that our results were comparable to standard LD findings, we based our stimuli on a previous dataset (Keuleers et al., 2010). Next, we performed a traditional behavioral analysis and calculated ERPs. Behavioral findings – RTs and error rates – displayed differences between all conditions in line with previous findings (Fiez et al., 1999; Table 3

The results of LME models for the duration of Stage 5.

| Reference level: HF | B     | SE    | t      | p       |
|---------------------|-------|-------|--------|---------|
| HF                  | 183.23| 8.27  | 22.16  | <0.001  |
| LF                  | 53.46 | 2.30  | 23.18  | <0.001  |
| Pseudo              | 111.96| 2.32  | 48.27  | <0.001  |
| Random              | -26.26| 2.27  | -11.58 | <0.001  |
| Reference level: LF | B     | SE    | t      | p       |
| Intercept           | 236.69| 8.27  | 28.60  | <0.001  |
| LF                  | 58.50 | 2.35  | 24.92  | <0.001  |
| Pseudo              | 79.71 | 2.29  | -34.68 | <0.001  |
| Random              | -138.22| 2.31  | 59.76  | <0.001  |
| Reference level: Pseudo | B     | SE    | t      | p       |
| Intercept           | 295.19| 8.28  | 35.65  | <0.001  |
| Random              | -138.22| 2.31  | 59.76  | <0.001  |

Fig. 5. The resulting HsMM-MVPA model where the duration of Stage 5 and Bump 5 differ across conditions. A. The first four topologies represent the amplitude of the bumps that are shared across all conditions, while the fifth bump is plotted separately for each condition. The bars below the topologies represent the average stage durations across participants and trials. B. The stage durations accompanied by within-subject standard errors (black lines) for each condition: HF (high frequency), LF (low frequency), Ps (pseudowords) and Rnd (random non-words).

Fig. 6. A comparison of the amplitude of Bump 5 across conditions (row > column, e.g. HF > LF). The displayed topologies represent t-values for the significant differences that were corrected for false discovery rate (FDR; p < 0.01). The values for non-significant differences (p > 0.01) were set to 0.
Consistent with the literature, ERP results indicated two main components associated with these differences in RTs, the N400 and P600 (Carreiras et al., 2005; Holcomb & Neville, 1990).

To identify cognitive stages, the HsMM-MVPA analysis was applied to the EEG data, providing evidence for 5 bumps and 6 stages for all four conditions. While most of these stages were shared, Stage 5 and the consecutive Bump 5 were found to differ between conditions. The duration of Stage 5 was different for all conditions, while the amplitude of Bump 5 was greater for HF and LF items than for pseudowords. This leads to our first main conclusion: both the word frequency effect and the nonword lexicality effect originate in a single stage.

Based on the brain activations and durations, the discovered stages were further interpreted concerning the underlying cognitive processes. Stages 1–2 highly resemble the stages from other HsMM-MVPA studies where they were interpreted as pre-attention and early encoding stages (Anderson et al., 2016; Zhang, Walsh, & Anderson, 2017). This is in line with the findings on N100 and P200 components (Braun et al., 2006; Holcomb et al., 2002) and reading-related activations in occipito-temporal cortex and IFG (Murphy, Jogia, & Talcott, 2019; Wang et al., 2015) previously reported in LDT.

The topological distribution and the duration of Stage 3 mirror a P300 (P300a) component typically associated with the allocation of attentional resources elicited by the stimuli (Polich, 2007; Soltani & Knight, 2000). Evidence suggests that the amplitude of this component is inversely related to the amount of resources required for the task (Kok, 2001). While neural origins of P300a are still not well defined, it was previously found that frontal lobe and hippocampus might play a role in its generation (Polich, 2007).

Stage 4 is identical to a familiarity-driven recognition stage previously reported in Berberyan et al. (2021). This pattern is consistent with familiarity-based theories where the familiarity of the stimulus was assumed to influence a consecutive lexical decision (Balota & Spieler, 1999; Wagenmakers et al., 2004; Zeelenberg et al., 2004). However, even though the familiarity of the words was probably judged in this stage, this did not affect the duration of the stage, in agreement with familiarity mechanisms in other tasks (e.g., Borst, Ghuman, & Anderson, 2016). The brain activation of this stage is compatible with recent ERP studies where familiarity was associated with frontal negativity (Curran, 1999; Woodruff, Hayama, & Rugg, 2006). fMRI studies have associated this activity with activation in prefrontal cortex (Aly, Yonelinas, Kishiyama, & Knight, 2011; Horn et al., 2016). However, an prominent alternative view argues that familiarity is related to the medial temporal lobe (e.g., Borst et al., 2016; Eichenbaum, Yonelinas, & Ranganath, 2007; Norman & O’Reilly, 2003).

The next question concerns the function of Stage 5. First, Stage 5 is the penultimate stage, which implies that it does not include motor preparation, as that is most likely located in the final stage. Second, in a previous study in which we experimentally manipulated decision difficulty, we saw a very similar bump-stage-bump pattern (Berberyan et al., 2021). In that study, the onset bump of the decision stage showed strong frontal negativity, and the end of the decision stage strong central-
parietal positivity – highly reminiscent of the current bump topologies of bumps 4 and 5. When translating these findings to the current task, it implies that Stage 5 is a decision stage, where the difficulty of the decision determines the duration of the stage, as well as the amplitude of Bump 5.

The current patterns are in line with the conventional P300b effect, which is known to vary with response confidence, with higher confidence leading to more positive P300b responses (Borst & Anderson, 2013; Nieuwenhuis, Aston-Jones, & Cohen, 2005; Sutton, Ruchkin, Munson, Kietzman, & Hammer, 1982). This suggests that the decision was most difficult for pseudowords, which is corroborated by the RT and error rate results. On the level of the neural structures, these results are compatible with previously discussed fMRI results where bilateral postcentral gyr, supplementary motor area, and right cerebellum were reported in LDT representing task-specific decision and motor planning (Carreiras, Meckell, et al., 2007).

Taken together, our findings are consistent with the previously discussed view that performance differences in the LDT can be best explained by differences in decision making, i.e., Balota & Chumbley, 1984; Besner, 1983; McCann et al., 1988; Ratcliff et al., 2004; Seidenberg & McClelland, 1989; Wagenmakers et al., 2004). Balota and Chumbley (1984) represented this decision process by a two-stage model where the first stage corresponded to a quick initial global computation of familiarity and the second - more analytical evaluation leading to decision. This “familiarity” process can be viewed as a result of various sources of lexical information such as orthographic, phonological and semantic information (Plaut, 1997). Continuing this idea, Ratcliff et al. (2004) suggested that these sources of information produce differences in a single component of drift diffusion model (DDM): drift rate, which has been typically associated with a decision (e.g., Mulder, van Maanen, & Forstmann, 2014). While these interpretations were based on theoretical assumptions rather than driven by data, in the current study, we assessed the exact cognitive stage that accounted for the differences. Interestingly, our results suggest that while stage 4 determines the familiarity of the words, this is only used as input for a decision process in stage 5.

The extension of ERPs, BRPs, showed that this decision process was located between two commonly identified ERPs: the N400 and P600. The larger N400 amplitudes for pseudowords compared to words in LD were previously explained through a lexical identification process (Meade, Grainger, & Holcomb, 2019). Because a lexical representation of pseudowords does not exist, the lexical identification process requires additional effort. These ideas can be integrated with the decisional account by assuming that the lexical identification process feeds into the decision. Here, the N400 might signify the starting point of the decision process – with different levels for the different conditions.

Additionally, the BRPs showed that not only the amplitude of the P600 differed between conditions but also its latency. While the P600 has been commonly found in language studies, there is an ongoing discussion on its interpretation and relation to other extensively studied positive-going component, the P300b (Polich, 2007). According to one of the views, these components are overlapping and share their functional interpretation (for an overview, see Leckey & Federmaner, 2020). Because the P300b is commonly associated with decision making and appears in binary decision tasks (Kutas, Van Petten, & Klunder, 2006; Twomey, Murphy, Kelly, & O’Connell, 2015), this fits with our explanation of Stage 5 as a decision stage. Note that there is an alternative explanation where the two components are assumed to be independent of each other with different neuronal generators (Frisch, Kotz, von Cramon, & Friederici, 2003).

Although in LD studies the N400 and P600 components were mostly reported in isolation, a recent study suggested an integrated functional interpretation of these components (Deogu, Brouwer, & Crocker, 2019). To this end, they were interpreted as part of a single process (labelled Retrieval-Integration account, see Brouwer, Fitz, & Hoeks, 2012) with the N400 indicating memory retrieval and the P600 semantic integration. While this study established the importance of integration of these components, it is difficult to translate these findings on our data where the words were studied in isolation rather than in the context of sentences. That said, our study showed that these components should be studied together, as the latency between those components seems to be responsible for the overall RT effects in lexical decision.

Finally, there have been various approaches to model the word recognition process in LDT. In the past, DDM represented the standard approach to modeling data from this task (e.g., Donkin & Heathcote, 2009; Ratcliff et al., 2004; Tillman et al., 2017). While DDM allows decomposing data into decision and non-decision time, it does not lead to exactly the same conclusions as HsMM-MVPA does: where the HsMM-MVPA method attributed all condition effects to a single decision stage, some DDM results also indicate non-decision time differences (Donkin & Heathcote, 2009; Gomez & Perea, 2014). An important reason for that is the different sources of information that enter the model, namely, a single reaction time value per trial in the case of DDM and many EEG samples per trial in the case of HsMM-MVPA. While different variability in RTs per condition might lead to differences in non-decision time estimates in DDM modeling, the HsMM-MVPA method locates the same bumps on each trial, theoretically resulting in better stage length estimates. However, this is naturally dependent on the quality of the data, and EEG data might incorporate more noise than behavioral data. In our recent work, we discuss in more detail some differences in non-decision time estimations resulting from these methods (Berberyan et al., 2021).

5. Limitation and future research

It should be noted that while both ERPs and HsMM-MVPA results indicated that the main difference between conditions started around 400 ms post-stimulus, the ERPs also showed slight differences between random non-words and other conditions starting around 200 ms at P8 and F7. However, these differences were limited to the amplitude of the signal, and were not observed in the temporal location of the peaks. The HsMM-MVPA method attempts to find bumps, and assumes no amplitude differences in the flats between consecutive bumps (Anderson et al., 2016; van Maanen et al., 2021). Given that the amplitude differences are also still visible in the BRPs (Fig. 7), this assumption is not fully met here. This suggests that there is a (small) processing difference for random strings, but that this processing difference does not result in a difference in stage topology or duration (see Model selection), at least not one that can be detected in the current dataset.

Additionally, HsMM-MVPA analysis relies on the assumption that cognitive stages are shared across participants and trials (van Maanen et al., 2021). While the current implementation of the method allows for flexibility in the duration of the stages, it is not aimed at exploring individual differences due to the absence of subject-specific parameters. We believe that the method could be further extended to include inter-individual variability. Such an extension would, for example, allow observing how the individual differences in lexical familiarity influence lexical decision.

While the current findings implicate differences between conditions in later stages, these stages might not be fixed and could be modulated by an attentional factor. In a recent study, a word frequency manipulation resulted in much earlier ERP differences in a go/no-go version of LDT than in a standard LDT (Vergara-Martinez, Gomez, & Perea, 2020). This was interpreted as relocation of attentional resources towards stimulus processing compared to a standard LDT (Smid, Fiedler, & Heinze, 2000). For HsMM-MVPA models it might mean that the observed difference in conditions would be present in stages other than decision, or that the decision stage would occur earlier. Altogether this highlights an important direction for a future HsMM-MVPA application.

6. Conclusion

In conclusion, we investigated cognitive processes underlying LD
using a data-driven approach, namely, HsMM-MVPA applied to EEG data. We found that commonly reported main effects of word frequency and nonword lexicality were located in a single processing stage. The onset and termination of this processing stage overlapped with two language-related ERP components: the N400 and P600. Based on its temporal location and brain activation, this stage was interpreted as a decision process.

CRediT authorship contribution statement

Hermine S. Berberyan: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. Hedderik van Rijn: Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. Jelmer P. Borst: Conceptualization, Resources, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank Rosa Verhoeven for her help with data collection and Oscar Portoles for his helpful suggestions on HsMM-MVPA analysis.

Funding sources

Van Rijn was supported by the research programme “Interval Timing in the Real World: A Functional, Computational and Neuroscience Approach,” with Project Number 453-16-005, financed by the Netherlands Organisation for Scientific Research (NWO).

Code availability

The code required to reproduce the analyses is available at http://osf.io/z49me/.
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