Lexical-semantic and executive deficits revealed by computational modelling: A drift diffusion model perspective

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ARTICLE INFO

ABSTRACT

Flexible language use requires coordinated functioning of two systems: conceptual representations and control. The interaction between the two systems can be observed when people are asked to match a word to a picture. Participants are slower and less accurate for related word-picture pairs (word: banana, picture: apple) relative to unrelated pairs (word: banjo, picture: apple). The mechanism underlying interference however is still unclear. We analyzed word-picture matching (WPM) performance of patients with stroke-induced lesions to the left-temporal (N = 5) or left-frontal cortex (N = 5) and matched controls (N = 12) using the drift diffusion model (DDM). In DDM, the process of making a decision is described as the stochastic accumulation of evidence towards a response. The parameters of the DDM model that characterize this process are decision threshold, drift rate, starting point and non-decision time, each of which bears cognitive interpretability. We compared the estimated model parameters from controls and patients to investigate the mechanisms of WPM interference. WPM performance in controls was explained by the amount of information needed to make a decision (decision threshold): a higher threshold was associated with related word-picture pairs relative to unrelated ones. No difference was found in the quality of the evidence (drift rate). This suggests an executive rather than semantic mechanism underlying WPM interference. Both patients with temporal and frontal lesions exhibited both increased drift rate and decision threshold for unrelated pairs relative to related ones. Left-frontal and temporal damage affected the computations required by WPM similarly, resulting in systematic deficits across lexical-semantic memory and executive functions. These results support a diverse but interactive role of lexical-semantic memory and semantic control mechanisms.

1. Introduction

Flexible language use requires coordinated functioning of two systems: conceptual representations and control (Lambon Ralph et al., 2017). The system of conceptual representations entails a distributed network of cortical regions that code information multi-modally (Barsalou, 2008; Warrington and Shallice, 1984) and allow to generalize to new knowledge thanks to already existing representations (Patterson et al., 2007; Rogers et al., 2004). The control system manipulates the semantic knowledge depending on the task at hand (Hoffman et al., 2013; Thompson-Schill et al., 1997). Understanding the contributions of control mechanisms to lexical-semantic processes is an important theoretical question, with potential applications for clinical research.

Control mechanisms (henceforth referred to as semantic selection) operate over several automatically activated semantic representations to ensure the functioning of semantic cognition (Lambon Ralph et al., 2017). Multiple co-activated semantic representations can result in competition depending on the semantic selection demands in the context of a task (Chiou et al., 2018; Jefferies et al., 2010). Competition between (lexical-) semantic representations can manifest itself via semantic interference in tasks such as word-picture matching (Campanella and Shallice, 2011; Crutch and Warrington, 2005) or picture-word interference (Lupker, 1979; Piai and Knight, 2018). Semantic interference is reflected in poorer performance when comparing semantically related word-picture pairs to unrelated ones. For example, participants are slower when they have to match a picture preceded by a related word (word: "banana", picture: apple) as opposed to an unrelated word (word: "banjo", picture: apple). While various psycholinguistic studies

propose theoretico-computational accounts of interference effects in language production using picture naming paradigms (Howard et al., 2006; Oppenheim et al., 2010; Roelofs, 2018, 1992), mechanistic explanations of this effect in language comprehension using word-picture matching types of tasks are scarce. Most of the computational models in the language production literature that could be extended to explain semantic interference in word-picture matching are neural network models that operate at the level of the excitatory-inhibitory connections between conceptual and lexical nodes (Howard et al., 2006; Oppenheim et al., 2010; but see Roelofs, 2003). It is generally accepted that in addition to lexico-semantic processes, executive mechanisms govern the extraction of relevant semantic information from stimuli (Badre et al., 2005; Jefferies and Lambon Ralph, 2006; Lambon Ralph et al., 2017; Nagel et al., 2008). The exact mechanisms – lexico-semantic and/or control – governing retrieval and selection in competitive semantic contexts are still not clear.

In this study, we investigated the task demands elicited by competing semantic representations using a word-picture matching paradigm, in which participants verify whether a word and a subsequently presented picture match. Behavioral performance was then modelled using the drift diffusion model (DDM, Ratcliff, 1978), an analytical approach that combines reaction time distributions for correct and incorrect task responses in order to estimate latent variables associated with task performance. According to the DDM framework, any binary decision-making task is described as a stochastic accumulation of evidence over time towards one of the two decision boundaries (Fig. 1). Once the decision is reached, then the response associated with that boundary is produced (Voss et al., 2013a,b). In the DDM, a total of four parameters describe the components underlying decision making: the rate with which evidence accumulates over time (*drift rate*), the amount of evidence that is necessary to reach a response (*decision threshold*), the amount of information accumulated before the decision process has started (*starting point*) and the time required by *non-decision processes*, such as motor preparation or stimulus encoding. Moreover, we applied the DDM approach not only to decision-making data from neurotypical participants, but also to data from individuals with frontal or temporal lobe lesions. The lesion approach can help further clarify the

relationship between the latent variables and the presupposed cognitive levels. In addition, we used a hierarchical version of DDM (HDDM) where model parameters were estimated in a Bayesian framework, allowing for accurate model fits even with relatively few trials. This approach provides a great advantage for the analysis of data from clinical populations, where collecting thousands of experimental trials for an accurate model fit (Brunton et al., 2013) is unfeasible.

Previous psycholinguistic experiments that applied drift diffusion formalism showed that the drift rate reflects processes operating at the level of lexical semantics. For example, a larger drift rate was found for words in comparison to random letter strings but not in comparison to word-like non-words (Ratcliff et al., 2004a,b). Moreover, words of higher frequency had a higher drift rate compared to words of lower frequency (Ratcliff et al., 2004a,b). Semantic priming experiments with lexical decision brought additional evidence that the drift rate serves as a proxy for processes related to lexico-semantic representations (Meyer and Schvaneveldt, 1971; Neely, 1991; Wentura, 2000). Particularly, during lexical decision, related word-target pairs (word: "lion", target: tiger) resulted in a higher drift rate as opposed to unrelated targets (word: "king", target: bee). Interestingly, the results remained similar even when changing the task from lexical to semantic decision, i.e., when participants had to decide if the target was a living entity (Voss et al., 2013a,b). This finding was interpreted in terms of semantic facilitation of lexical access. The fact that lexicality, word-frequency, and semantic priming effects are reflected in the drift rate is an indication that the drift rate reflects lexical-semantic processes.

In the field of decision making, it has been consistently shown that modulation of the decision threshold is directly related to how cautiously people behave (Bogacz et al., 2010; Forstmann et al., 2010). For example, if participants prioritize accuracy over speed in their responses then the decision threshold is raised, i.e., it takes more time to accumulate information towards one decision threshold (responses are slow but accurate). The decision threshold is modulated by conflict tasks, being higher for the most conflicting conditions in comparison to the less conflicting ones (Cavanagh et al., 2011). Moreover, in traditional executive tasks, such as the Stroop task, the decision threshold is associated with mechanisms of executive control (Kinoshita et al., 2017).

While the number of studies that applied DDM modelling to experiments investigating aspects of lexico-semantic retrieval is modest, they bring indicative results about the relevance of the decision threshold. For example, Anders and colleagues showed that increasing semantic interference in a blocked-cyclic picture naming task resulted in decrease of lexical accumulation activity (drift rate) and increase in the amount of activation necessary for lexical target selection (threshold) for healthy subjects (Anders et al., 2017). Crucially, patients with prefrontal lesions failed to adjust the decision threshold appropriately in comparison to controls (i.e., no up-adjustment for the most interfering condition). Anders et al. highlight that patients with prefrontal lesions have impaired selection processes in word production (Schnur et al., 2009), that can potentially be more domain-general (Ries et al., 2014, 2015). We note that the discussion about the nature of the control mechanisms in the context of language tasks is still ongoing, and it is outside the scope of the present study to contribute to that debate (Hoffman, 2018; Noonan et al., 2013; Thompson-Schill et al., 1997).

Neuropsychological evidence for semantic cognition posits that processes of semantic knowledge and control have different neural substrates. While anterior and ventro-lateral parts of left temporal lobe are crucial for semantic knowledge (Hickok and Poeppel, 2004; Patterson et al., 2007), left prefrontal regions are associated with semantic retrieval (Lambon Ralph et al., 2017; Noppeney et al., 2004). Indeed, previous studies investigating the role of left prefrontal cortex (PFC) in word selection showed that left PFC helps overcome semantic interference by boosting mechanisms of control (Ries et al., 2014), especially when selection demands are difficult (Ries et al., 2015). However, PFC involvement may be dependent on the task and individual variability
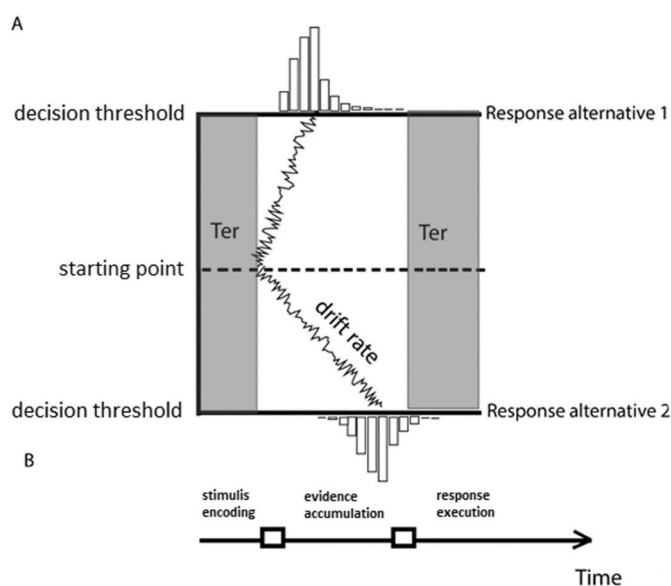

Fig. 1. Schematic representation of the drift diffusion model. Once the stimulus is encoded, the process of evidence accumulation begins. The evidence is accumulated towards one of the decision boundaries. After the boundary is reached, the response is executed. We adopted the following notation for the model parameters description: non-decisional component (T_{er}), drift rate (v), decision threshold (A), starting point (z).

([Piai and Knight, 2018](); [Piai et al., 2016](); [Python et al., 2018]()). Recently, it has been proposed that prefrontal regions, in particular the inferior frontal gyrus (IFG), operate in conjunction with the posterior middle temporal gyrus (MTG) contributing to the mechanisms of semantic control ([Davey et al., 2016](); [Whitney et al., 2012]()). Understanding the mechanisms of impairment in semantic retrieval and selection is still an ongoing task for the language community.

We investigated the processing stages of semantic interference in healthy participants and patients with left temporal or frontal lesions. We used a word-picture matching task (i.e., participants indicated whether the word and the picture matched), where the picture was preceded by related words (word: "banana", picture: apple), unrelated words (word: "banjo", picture: apple) or words that directly denoted the picture (word: "apple", picture: apple). We had the following hypotheses regarding the experimental results. First, the interference effect can be reflected in the drift rate, which would support the idea that the interference resides at the lexico-semantic level. We would expect the drift rate to decrease for the related pairs as opposed to the unrelated pairs, following the finding that semantic interference in blocked-cyclic naming is reflected in decreased drift rate ([Anders et al., 2017]()). We note that this prediction is contrary to the semantic priming findings ([Voss et al., 2013a,b]()). Alternatively, or in addition to the effects at the level of evidence accumulation (drift rate), the interference effect can modulate the decision threshold, reflecting the amount of information needed to reach the decision. In this case, we would expect higher threshold for the condition that evokes more interference i.e., related relative to unrelated word-target pairs. We note that this prediction is both in line with [Anders et al. (2017)](), and follows the logic of conflict tasks ([Cavanagh et al., 2011](); [Kinoshita et al., 2017]()). This would support the idea that executive control is involved in the presence of semantic competition, which is strengthened by the semantic relationship between the picture and the word. After having established the mechanisms of semantic interference in healthy participants, we compared the interference effect between healthy subjects and the individuals with left frontal or temporal stroke-lesions. Due to the fact that patients with temporal lesions had a combination of lesions in both anterior and posterior sites of MTG, we expected a joint effect of semantic competition on the drift rate and decision threshold reflecting deficits at potentially both lexico-semantic and executive levels. For the patients with frontal lesions, we would expect deficits in the decision threshold as it reflects strategic cognitive control allocation ([Cavanagh et al., 2011](); [Domenech and Dreher, 2010]()). Damage to the frontal cortex might also lead to the deterioration of the activation levels in the lexico-semantic domain (which would be reflected in decreased drift rate) due to the connected frontal and temporo-parietal networks that underlie semantic control ([Lambon Ralph et al., 2017]()).

To sum up, we investigated the contribution of control mechanisms during semantic retrieval and selection in healthy adults and adults with stroke-induced lesions using a word-picture matching task and computational modelling (HDDM). With that, we add to an existing body of literature that combines computational modelling with a lesion mapping approach, which provides a promising avenue towards formalizing brain-behavior relations ([Chen et al., 2018](); [Dell et al., 2007](); [Hoffman et al., 2018]()).

2. Methods

2.1. Participants

Twelve patients with stroke-induced lesions to the left lateral-temporal or lateral-frontal cortex participated (five females; median age = 66, mean = 65, sd = 9, range = 50–74; mean years of education = 17). One additional patient with Wernicke's aphasia was included, but failed to understand the instructions and testing was therefore discontinued. We differentiate patients with lesions in temporal and frontal lesions based on the topology of the predominant lesions. While patients

with temporal lesions had lesions predominantly in temporal areas (MTG, STG) but not in fronto-striatal regions, patients with frontal lesions had lesions predominantly in frontal or striatal areas. We excluded two patients that had lesions in both temporal and fronto-striatal areas. Patients were tested at least 12 months post stroke and were premorbidly right-handed. Additionally, 12 right-handed controls participated, matched to the patients for gender (five females), age (within ±4 years of age, median age = 66, mean age = 64, sd = 8, range = 50–74, $t < 1$, $p = .873$), and years of education (±4 years of education, mean years of education = 17, $t < 1$, $p > .949$). All participants were native speakers of American English and none had a history of psychiatric disturbances, substance abuse, medical complications, multiple neurological events, or dementia. Information on the patients' lesions and language ability are shown in [Tables 1 and 2](). The study protocol was approved by the University of California, Berkeley Committee for Protection of Human Subjects, following the declaration of Helsinki. All participants gave written informed consent after the nature of the study was explained and received monetary compensation for their participation.

2.2. Lesion analysis

Lesions were drawn on patients' structural magnetic resonance images (MRIs) by a trained technician and confirmed by a neurologist. Lesions masks were then normalized to the MNI template. Percent damage to different areas was determined based on the Automated Anatomical Labeling template in MRIcroN ([Rorden and Brett, 2000]()). The maps of lesion overlap are presented in [Fig. 2](). In the patients with temporal lesions, the lesions were mostly present in the left middle temporal gyrus (100% overlap). In the patients with frontal lesions, the lesion overlap was centered on the left inferior frontal gyrus and left middle frontal gyrus (100% overlap).

Lesion distributions for each patient group are shown in [Fig. 2](). Five patients had lesions predominantly in the left frontal lobe and five in the left temporal lobe. Language scores ([Kertesz, 1982]()) were available for ten patients.

3. Materials

Seventy pictures were selected from the BOSS database ([Brodeur et al., 2010]()) together with their basic-level names. For each picture, three conditions were created. In the congruent condition, the prime word was the picture's basic-level name. For the semantically related condition, prime words were selected using existing norms ([Nelson et al., 2004]()). The forward strength between the prime word and the picture name ranged between 0.108 and 0.879 (mean = 0.451, median = 0.394, sd = 0.2). For the unrelated condition, prime word and target picture names were recombined to form semantically and phonologically unrelated pairs. The association norm in the unrelated condition was 0 for all items. Latent semantic analysis ([Deerwester et al., 1990]()) was also used to confirm the strength in semantic relationship between the prime word and the picture name (related condition: mean = 0.463, median = 0.42, sd = 0.212; unrelated condition: mean = 0.071, median = 0.05, sd = 0.071, $t(69) = 14.05$, $p < .001$). The prime words were spoken by a female native speaker of American English, recorded in a soundproof booth and subsequently normalized to 77 dB sound-pressure level.

3.1. Procedure

Stimulus presentation and response recording were controlled by Presentation® software (Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Participants were tested individually in a sound-attenuated, dimly-lit booth. The words were presented via loudspeakers. Participants responded with a left-hand button press, using the index finger for 'yes' responses and the middle finger for 'no' responses.

Table 1

Individual percent damage to the striatum (joint measures for caudate, putamen and globus pallidus), left inferior frontal gyrus (IFG: opercularis, triangularis, orbitalis), middle frontal gyrus (MFG, including middle orbital frontal), middle temporal gyrus (MTG, including middle and inferior MTG), superior temporal gyrus (STG) and parietal lobe (POST: Postcentral gyrus, SMG: Supramarginal gyrus, AG: angular gyrus, P2: inferior parietal gyrus, P1: Superior parietal gyrus).

Patient	Striatum	IFG	MFG	MTG	STG	POST	SMG	AG	P2	P1
Left temporal lobe lesions										
P 1	0	0	0	23.6	34.0	.2	12.5	2	0	0
P 2	0.1	0.2	0	31.5	67.4	12.6	85.1	.4	35.9	0
P 3	0	0.1	0	33.4	88.1	4.7	88.3	57.9	25.8	0
P 4	0	0	0	7.9	0.8	0	0	0	0	0
P 5	1.8	0	0	48.1	7.8	0	0	0	0	0
Left frontal lobe lesions										
P 6	81	93.4	53.3	0.1	1.3	4.4	0	0	0	0
P 7	30.53	78.03	37.21	0	10.1	6.1	0	0	0	0
P 8	23.8	57.9	27.9	0	49.8	58.2	71.6	.5	25.7	.2
P 9	0	6.1	7	0	0	2.4	0	0	0	0
P 10	33.3	57.2	4.75	0	12.9	0	0	0	0	0

Table 2

Language testing data from the Western Aphasia Battery (WAB). Naming = WAB Naming and Word Finding score (maximum = 10). Comprehension = WAB Auditory Verbal Comprehension score (maximum = 10). Aphasia Quotient (AQ, maximum = 100).

|	AQ	Naming	Comprehension
P 1	NA	NA	NA
P 2	63.9	7.9	8.55
P 3	92.9	9.5	9.55
P 4	99.6	10	10
P 5	94	8.6	10
P 6	91.6	9.2	10
P 7	92.05	9.3	8.825
P 8	87.2	8.9	8.9
P 9	NA	NA	NA
P 10	99.6	9.8	10

A trial began with a fixation cross displayed for 1 s. The fixation cross stayed on the screen during word playback and then during a silent period of 1 s between auditory word offset and picture onset. Then the picture was presented for 2 s and participants responded during this period. Three asterisks, indicating termination of the trial (***) then appeared for a variable interval between 1.2 and 1.9 s. An example of an experimental trial is given in Fig. 3. There were 280 experimental trials (70 for each of the related and unrelated conditions, and 140 for congruent condition).

3.2. Analysis

The behavioural data and the analysis scripts are available on the OSF (see "Data Availability Statement" below).

3.3. Behavioral analysis

We analyzed the reaction times (RT) and the accuracies for the following three comparisons: related vs. unrelated, related vs.
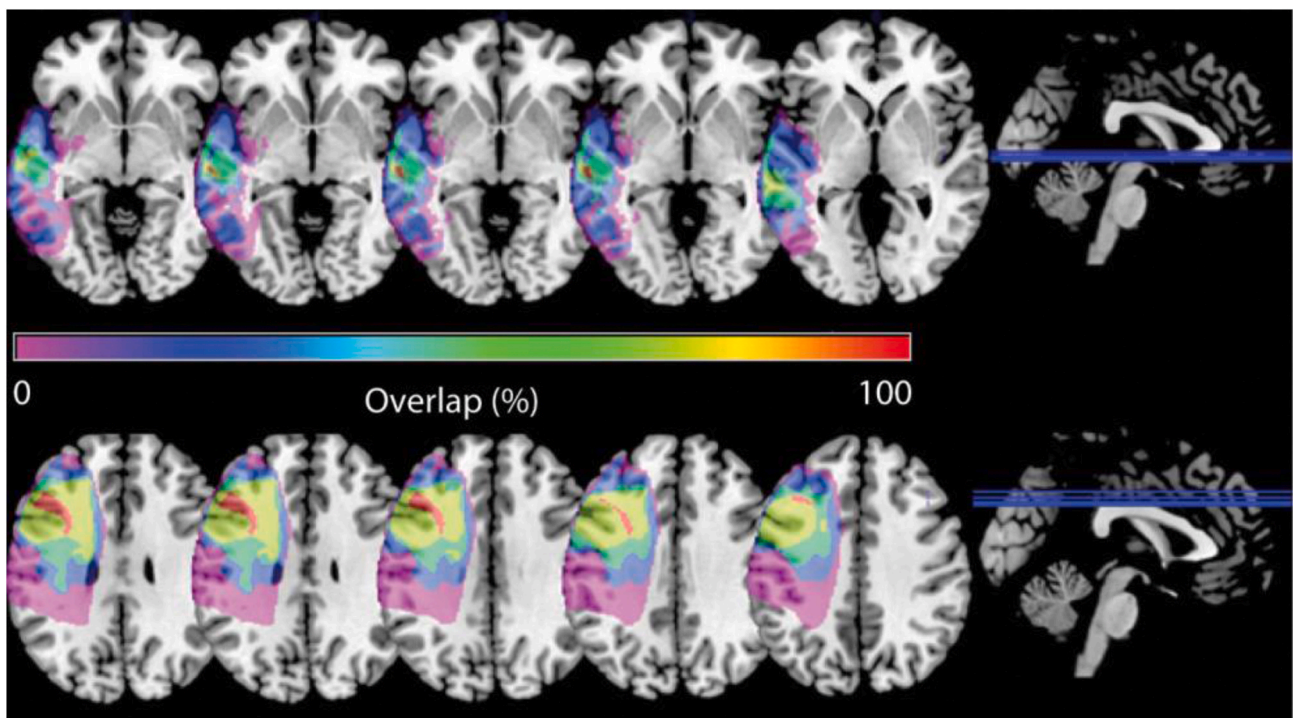
Fig. 2. Upper. Lesion overlap of individuals with temporal lobe lesions (100% overlap in left middle temporal gyrus). Lower. Lesion overlap of individuals with frontal lobe lesions (100% overlap in left inferior and middle frontal gyrus).
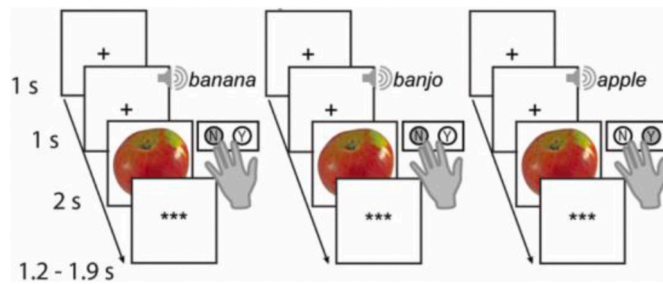
Fig. 3. Trial structure. Examples are given for a related (left), unrelated (middle), and congruent (right) trials.

congruent, unrelated vs. congruent. The related vs. unrelated conditions are the main focus of our investigation as they provide a cleaner contrast of lexico-semantic competition, had the same number of trials per condition, and required the same 'no' response. The other two contrasts involving the congruent condition are reported for completeness. However, we note that these comparisons are more problematic. They involve different responses (and response buttons) and they had different number of trials (the congruent condition twice as many). Moreover, certain pictures with lower name agreement were responded to with 'no' in the congruent condition more often than expected. Finally, and most importantly, these contrasts do not isolate lexico-semantic competition as clearly and the congruent condition has converging information at various levels of representation (conceptual, lexical, phonological), making it very different from the other two conditions. Reaction times were analyzed via analysis of variance (ANOVA) with word-picture relatedness (related, unrelated and congruent) and subject type (patients and controls) as factors. Accuracy was analyzed via log-linear regression analysis with word-picture relatedness (related, unrelated and congruent) and subject type (patients and controls) as factors. The analyses were performed using JASP (JASP Team, 2018).

3.4. Hierarchical drift diffusion model

It has been recently proposed that evidence accumulation is a plausible theoretical and empirical model of processes of lexico-semantic retrieval (Anders et al., 2017). We analyzed choice reaction time data with the hierarchical drift-diffusion model. The hierarchical Bayesian framework provides simultaneous estimation of individual and group subject parameters, which leads to robust model parameter estimates that better account for variability, especially in the performance of patients (Wiecki et al., 2013). Another advantage is the ability to obtain accurate model fits to the data using fewer trials, an extremely important aspect when investigating clinical populations. This makes HDDM an appropriate analytic tool for patient-based studies such as the current one (Ratcliff and Childers, 2015). We carried out the analysis using the Python toolbox HDDM 0.6.0 (Wiecki et al., 2013). We fitted models with different combinations of free parameters to the data via Markov Chain Monte Carlo (MCMC) fitting routines. We coded as "correct" a 'no' response in the related and unrelated conditions, and a 'yes' in the congruent condition. As commonly done using HDDM (Cavanagh et al., 2011; Zhang et al., 2016.), for each model we assessed a) the convergence rate of the numerical fitting routines and b) the ability of the model to capture the observed RT distributions. We excluded from further analysis the models that failed to reach convergence or failed to capture the observed RT distributions. Finally, we compared the models of interest by computing the relative Deviance Information Criterion (DIC), which provides a measure of the goodness of the model fit to the data while penalizing model complexity (Schwartz, 2007). Further, for the best fitting model, we examined the differences in posterior estimates by conducting a Bayesian ANOVA (since the model parameters are inherently not statistically independent) with type of participant and

degree of semantic relatedness as factors. In the Bayesian framework, a Bayes factor (BF) provides graded evidence in favor or against the tested hypothesis (Wagenmakers et al., 2018). The evidence in favor of the alternative hypothesis (H_1) as opposed to the null hypothesis (H_0) has a subscript of 10 in the Bayes factor abbreviation BF_{10}, that is the evidence in favor of the alternative hypothesis. The following range from Kaas and Raftery (Kass and Raftery, 1995) facilitates interpretation of the Bayes factor: $BF_{10} = 1$–3 indicates "anecdotal" ("not worse more than a bare mention") evidence for H_1 compared to H_0; $BF_{10} = 3$–20 indicates "positive" evidence for H_1 compared to H_0; $BF_{10} = 20$–150 indicates "strong" evidence for H_1 compared to H_0; $BF_{10} > 150$ indicates "very strong" evidence for H_1 compared to H_0. We will only consider "strong" and "very strong" evidence for interpretation of our findings.

4. Results

4.1. Behavioral analysis

The results of RT and accuracy analyses are summarized in Figs. 4 and 5. In all subjects, word-picture relatedness (related, unrelated, congruent) modulated the RTs (main effect: $F(2, 6583) = 238.26$, $p < .001$). Details of the statistical results for the post-hoc comparisons are presented in Table 3. Post-hoc comparisons revealed significant differences between the related and unrelated conditions (mean difference = 92.61). We also found that performance depended on the subject type (main effect: $F(2, 6583) = 26.62$, $p < .001$). We did not find an interaction between word-picture relatedness and subject type, $F(4, 6583) = 0.59$, $p = .66$. For the remaining post-hoc comparisons, we found a difference for related vs. congruent (mean difference = 196.33) and unrelated vs. congruent (mean difference = 103.73).

We performed a log-linear regression to test the effects of word-picture relatedness and subject type on accuracy. Accuracy was marginally not modulated by subject type (main effect of subject: Deviance (2, 6589) = 5.74, p = .057). Word-picture relatedness was not significant: Deviance (2, 6587) = 4.03, p = .13). We did not find any significant interaction between type of subject and semantic relatedness: Deviance (4, 6583) = 1.18, p = .88).

4.2. Hierarchical diffusion modeling

4.2.1. Model convergence and model fit

We performed an outlier-removal on the data (fixed probability of 5%) before feeding it to HDDM. For all analyses, we set the MCMC (Gelman & Rubin, 1992) fitting routines to 20,000 iterations with a burn-in period of 10,000 iterations and a thinning of 5. We assessed model convergence by examining the posterior sample (no autocorrelation found, no "spikes" in the posterior trace per each of the conditions, see Fig. 6) and the R-hat statistic, which is a measure of convergence among multiple MCMC chains (three for the present study). Inspection of posterior density estimates revealed that the traces were stable over multiple samples, which indicated that the fitting routines have converged to a fixed estimate. The R-hat statistic under 1.1 indicated that chains with different starting values have converged to the same estimate. Successful convergence was confirmed also by a MCMC error for all of the parameters smaller than 0.01.

Finally, we evaluated the adequacy of each model's predictions by examining the predicted posterior quantiles for the RT distributions for each participant (Fig. 7).

Further, we quantitatively compared the models of interest by computing the associated DIC score for each model. According to DIC logic, a model with a lower DIC score is to be preferred to an alternative model with a higher DIC as the most parsimonious explanation of the data. Separately for patients and controls, we fitted seven variants of the model (see all model designs in Fig. 8).

First, we left drift rate, decision threshold, and non-decision time free to vary (Model 1, Fig. 8) over the type of word-picture relatedness
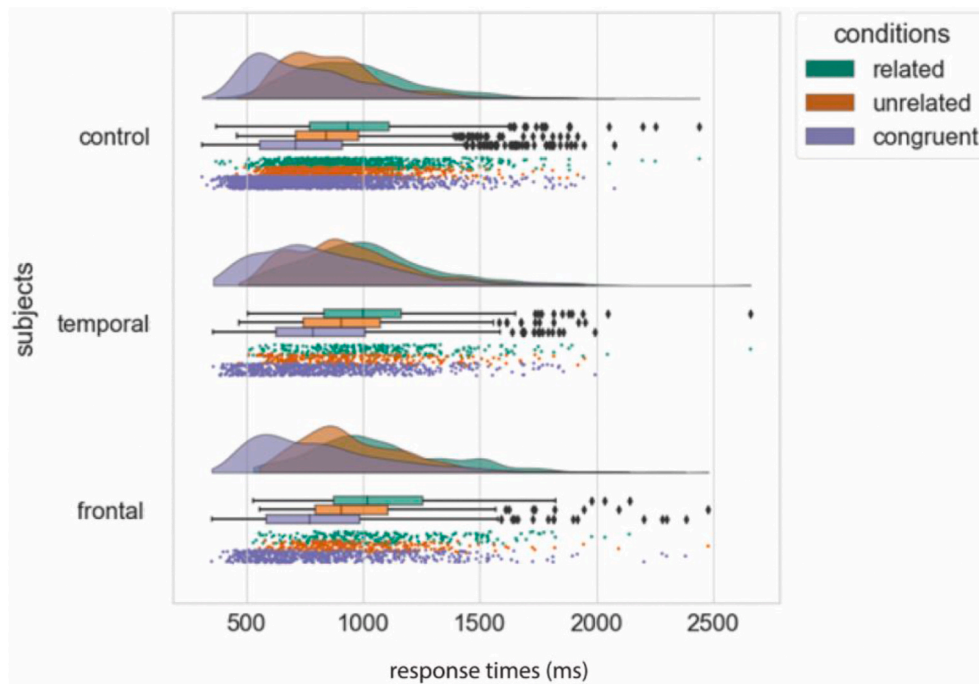
Fig. 4. Single-trial response times for all subjects and experimental conditions.
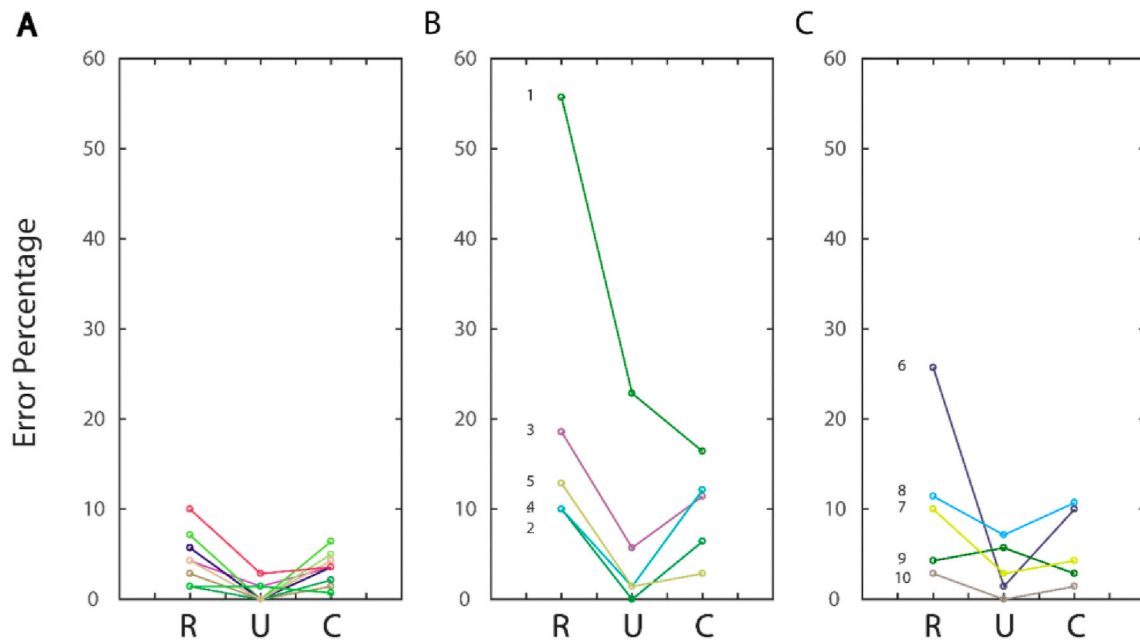

Fig. 5. Individual percentage of errors for control subjects (A), subjects with temporal lesions (B) and with frontal lesions (C). R – related, U – unrelated, C – congruent conditions.

Table 3
Post-hoc comparisons related to the main effects of picture relatedness and subject type.

Contrast: Reaction times	SE	t	p
related vs. unrelated	10.6	8.72	<.001
related vs. congruent	9.2	21.32	<.001
unrelated vs. congruent	9.09	11.41	<.001
frontal vs control	9.23	5.34	<.001
temporal vs control	9.04	6.43	<.001
frontal vs temporal	10.62	0.82	0.68

(related, unrelated, congruent). Then we fixed each of the parameters for the experimental factor of interest (semantic relatedness) across different models, leaving other conditions free to vary (Model 2–4, Fig. 8). Further, we fixed two parameters leaving one to vary (Model 5–7, Fig. 8). Next, we compared models with different combinations of parameters to find the most parsimonious account of the data. For both patients and controls, the model that best describes the data (i.e., the model with the lowest DIC score, see Table 4) was the model that allowed drift rate, threshold and non-decision time free to vary across the type of word-picture relatedness condition (Model 1 in Fig. 8). Conventionally, a DIC difference of more than 10 indicates that the
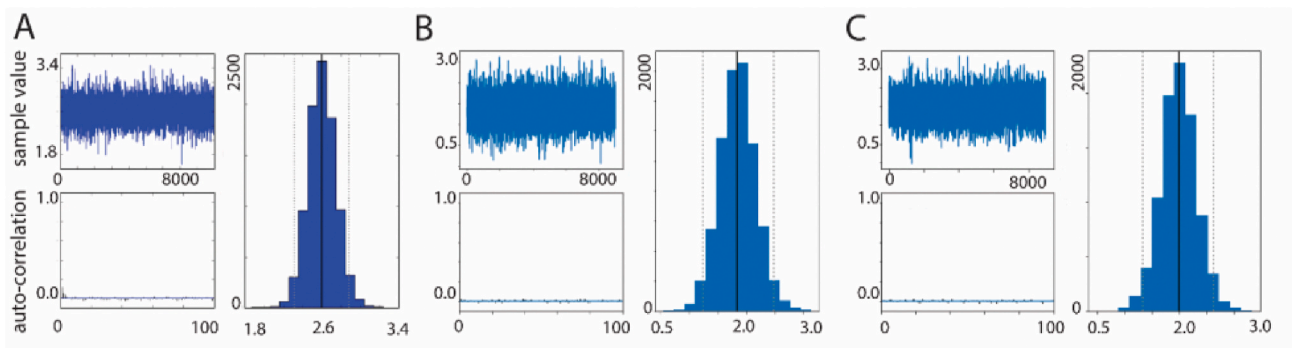
Fig. 6. Example of a converged chain for control subjects (A, dark blue) and patients (light blue) with temporal lesions (B) and frontal lesions (C). For each of the panels, top left: posterior trace, bottom left: autocorrelation, right: posterior histogram (solid black lines denote posterior mean and dotted black lines denote 2.5 and 97.5 percentiles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
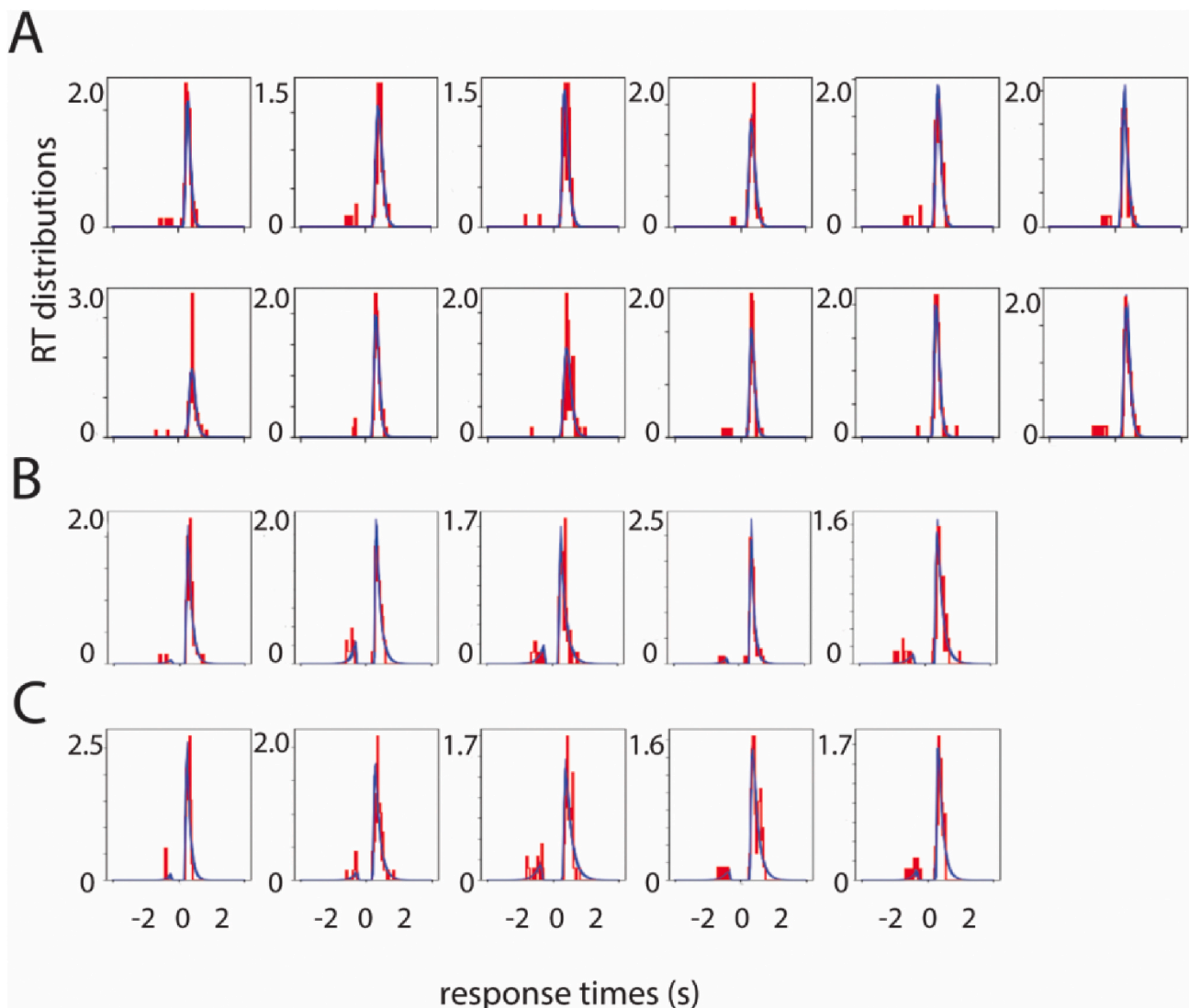

Fig. 7. Observed RT distribution (red lines) and predicted posterior (blue line) for (a) control subjects, (b) subjects with temporal lesions and (c) frontal lesions. The related condition is shown in all panels. Negative RTs represent trials in which the response was incorrect. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

evidence in favor of the model-winner is substantial (Burnham and Anderson, 2002).

For the controls, the difference between the winning model (Model 1, DIC -272.78) and the second-best model (Model 2, DIC -230.23) exceeded the difference of 10 by 4 times. For the patient group, the difference between the first (Model 1, DIC = 1228.60) and second-best
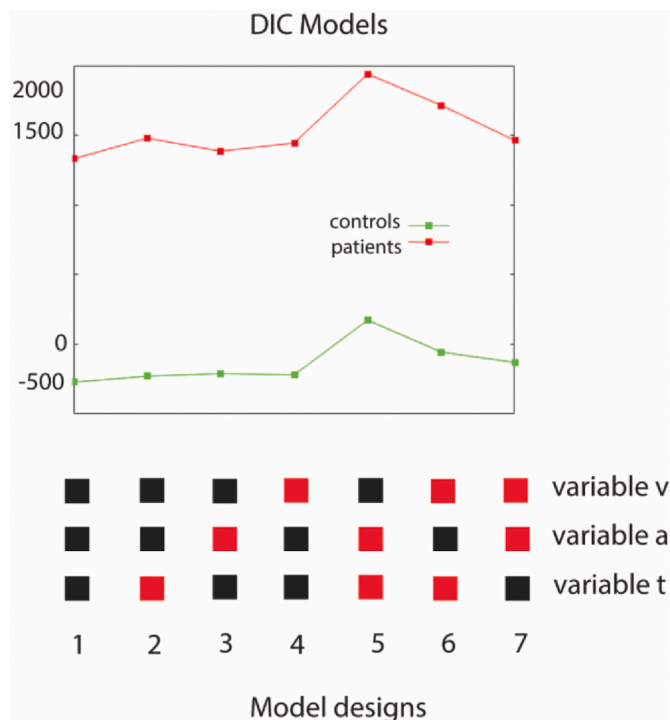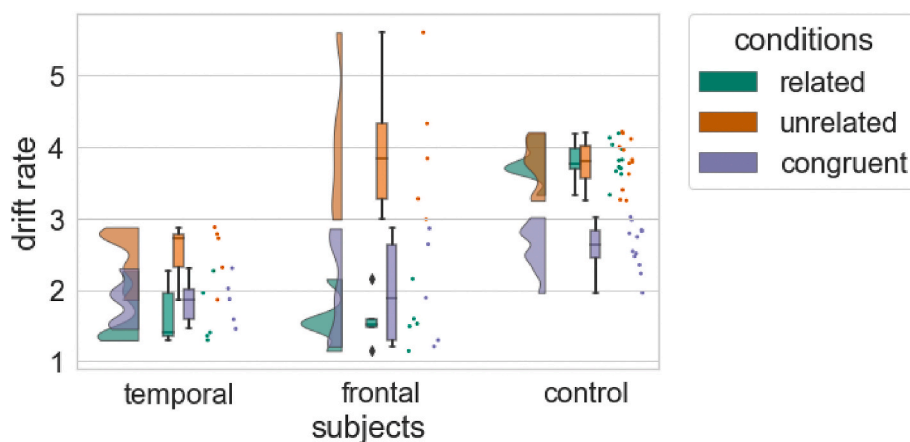
Fig. 8. The deviance information criterion (DIC) value for each of the competing models. The models differ according to the number of parameters free to vary over the experimental factor semantic relatedness (related, unrelated, congruent). Black squares indicate that a parameter is free, red squares mark fixed parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

model (Model 3 = 1280.11) exceeded the difference of 10 by 5. We consider this sufficient evidence for postulating that Model 1 best describes the data. Therefore, we carried out further analyses focusing on this winning model's parameters.

4.3. Model parameter analysis

4.3.1. Drift rate

Fig. 9 shows the drift rate estimates for each participant as a function of subject type and relatedness. A Jeffreys-Zellner-Siow (JZS, Liang et al., 2008; Rouder et al., 2012) Bayes factor ANOVA with default prior scales revealed that the best-fitting model consisted of main effects of word-picture relatedness, type of subject and an interaction between word-picture relatedness and type of subject. This model was preferred over the null model, $BF_{10} = 6.809e+14$ and over the second-best model that included main effects of word-picture relatedness and subject type, $BF_{10} = 2.099e+9$.

Further, we performed Bayesian paired samples t-tests for each subject type (controls, temporal, frontal) separately, which revealed the following differences in regards to the comparison of interest. In controls, the related and unrelated pairs were likely to be processed at the same drift rate (related vs. unrelated: $BF_{10} = 0.30$). For patients with temporal lesions, there was "positive" evidence in support of increased drift rate in unrelated relative to related conditions (unrelated > related: $BF_{10} = 11.32$). For the patients with frontal lesions, we found "very strong" evidence in favor of increased drift rate in unrelated relative to related conditions (unrelated > related: $BF_{10} = 48977$).

For completeness, we report the result for the additional contrasts. In control participants, we found that related pairs were likely to have higher drift rate as opposed to congruent pairs (related > congruent: $BF_{10} = 300221$). Similarly, unrelated pairs were more likely to have increased drift rate in comparison to congruent pairs (unrelated > congruent: $BF_{10} = 115.481$). For patients with temporal lesions, we found "anecdotal" evidence in favor of a difference between related vs. congruent pairs (related vs. congruent: $BF_{10} = 0.23$) and "positive" evidence in favor of increased rate in unrelated in comparison to congruent conditions, (unrelated vs. congruent: $BF_{10} = 7.83$). For the patients with frontal lesions, we found "strong" evidence in favor of increased drift

Table 4
Deviance information criterion for each model for patients and controls. For both controls and patients, the best winning model had variables drift rate, decision threshold and non-decision time free (Model 1, Fig. 8).

subject type/model	1	2	3	4	5	6	7
controls	-272.78	-230.23	-211.23	-219.83	173.21	-56.36	-131.01
patients	1228.60	1353.65	1280.11	1324.27	1762.66	1564.54	1336.42

Fig. 9. Posterior estimates of the hierarchical drift-diffusion model for the drift rate parameter. A difference in the related vs. unrelated condition was not detected in control participants, but was present in patients with both temporal and frontal lesions.

rate in unrelated in comparison to congruent conditions (unrelated > congruent: $BF_{10} = 62.60$), whereas related and congruent conditions showed "anecdotal" evidence supporting the condition differences (related vs. congruent: $BF_{10} = 0.85$). Additional analyses on selected groups of patients, reported in the Supplement, give further support to these findings.

In sum, we did not find reliable evidence supporting a difference in drift rate between related vs. unrelated contrast in control participants. By contrast, both temporal and frontal patients had increased drift rate for unrelated in comparison to related word-picture pairs.

4.3.2. Decision threshold

Fig. 10 shows the decision threshold estimates for each participant as a function of subject type and relatedness. A JZS Bayes factor ANOVA with default prior scales revealed that the model-winner was comprised of main effects of word-picture relatedness and type of subject, and their interaction. This model was preferred over the null model, $BF_{10} = 6.684e+24$ and over the second-best model that included main effects only $BF_{10} = 2.459e+6$.

In control subjects, we found "very strong" evidence that related pairs were more likely to have higher decision threshold as opposed to unrelated pairs (related > unrelated: $BF_{10} = 1.082e+8$). For the patients with frontal lesions, there was "very strong" evidence in favor of higher decision threshold in unrelated vs. related pairs (unrelated > related pairs: $BF_{10} = 48977$). Thus, the direction of the effect was reversed in comparison to the controls. For patients with temporal lesions, we found "strong" evidence in favor of increased decision threshold in unrelated compared to related conditions (unrelated > related: $BF_{10} = 43.06$). Once again, the direction of the effect was reversed in comparison to controls.

For additional contrasts, we found "very strong" evidence that control subjects were more likely to have higher decision threshold for related in comparison to congruent condition (related > congruent: $BF_{10} = 1.315e+7$). We also found "strong" evidence in favor of increased decision threshold for unrelated compared to congruent pairs (unrelated > congruent: $BF_{10} = 96.37$). For patients with frontal lesions, there was "very strong" evidence in favor of increased decision threshold for unrelated in comparison to congruent conditions (unrelated > congruent: $BF_{10} = 68985.08$). By contrast, the evidence supporting the difference between related and congruent conditions was "anecdotal", (related vs. congruent: $BF_{10} = 1.67$). We observed a similar pattern for patients with temporal lesions. We found "anecdotal" evidence in favor of the difference between related vs. congruent pairs (related vs. congruent: $BF_{10} = 0.80$), but "very strong" evidence in favor of increased decision threshold in unrelated vs. congruent conditions (unrelated > congruent: $BF_{10} = 307.52$). Additional analyses on selected groups of

patients, reported in the Supplement, give further support to these findings.

In sum, we found control subjects had a higher decision threshold for related as opposed to unrelated conditions. By contrast, the decision threshold was lower for related relative to unrelated word-picture pairs in both patient groups when compared to controls.

4.3.3. Non-decision component

Fig. 11 shows the non-decision component estimates for each participant as a function of subject type and relatedness. A JZS Bayes factor ANOVA with default prior scales revealed that the model-winner included main effects of word-picture relatedness, type of subject and their interaction. This model was preferred over the null model $BF_{10} = 2.178e+10$ and over the second-best model that included main effects of word-picture relatedness and subject type $BF_{10} = 828.436$.

We investigated the contrasts of semantic relatedness per subject group. In control subjects, there was "very strong" evidence in favor of decreased non-decision time in related as opposed to unrelated conditions (related < unrelated: $BF_{10} = 4.398e+6$). By contrast, in subjects with frontal lesions, there was "moderate" evidence for increased non-decision time for related in comparison to unrelated pairs (related > unrelated: $BF_{10} = 9.39$). We found "moderate" evidence in favor of the difference between related vs. unrelated pairs (related vs. unrelated: $BF_{10} = 6.57$) in participants with temporal lesions.

For additional contrasts, in control participants, we found "very strong" evidence in favor of decreased non-decision time in related as opposed to congruent conditions (related > congruent: $BF_{10} = 1912$). By contrast, more non-decision time was needed for unrelated than congruent conditions (unrelated > congruent: $BF_{10} = 31.38$). In subjects with frontal lesions, we found an "anecdotal" difference between unrelated vs. congruent conditions ($BF_{10} = 0.44$). We also found that less non-decision time was needed for congruent in comparison to related items (congruent > related: $BF_{10} = 28.01$). Patients with temporal lesions needed less non-decision time for congruent in comparison to related (congruent > related: $BF_{10} = 26.22$) and for congruent compared to unrelated items (congruent > unrelated: $BF_{10} = 22.27$).

In sum, control participants needed less non-decision time for related than unrelated conditions. By contrast, frontal patients had the opposite pattern: increased non-decision time for related than unrelated conditions. Temporal patients did not exhibit meaningful differences between related and unrelated conditions.

5. Discussion

This study investigated the mechanisms that contribute to semantic control in healthy participants and participants with lesions in left
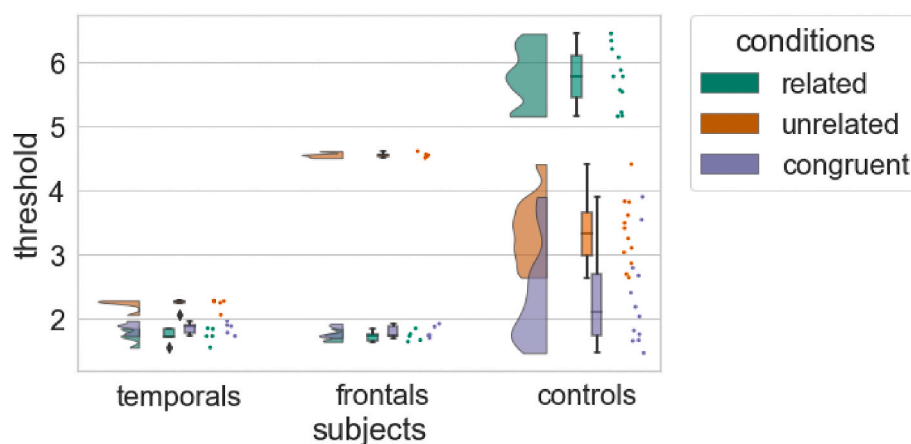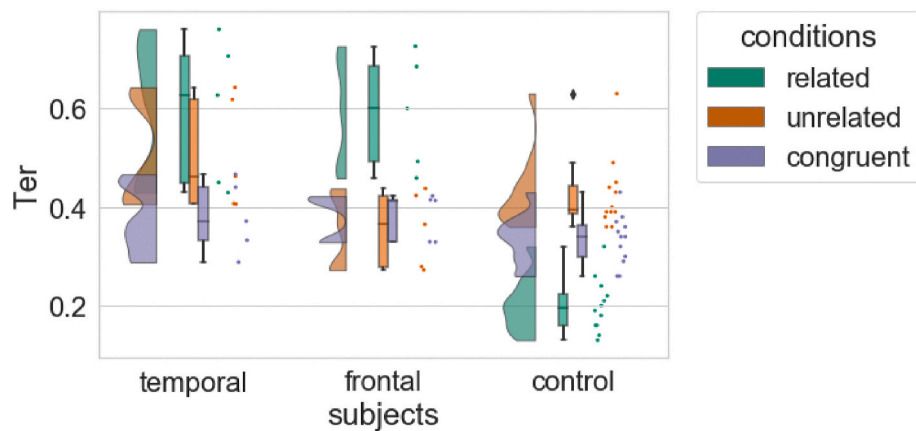

Fig. 10. Posterior estimates of the hierarchical drift-diffusion model for the decision threshold parameter. Related vs. unrelated differences in decision threshold had the opposite directionality for control participants versus participants with temporal or frontal lesions.

Fig. 11. Posterior estimates of the hierarchical drift-diffusion model for the non-decision time parameter (Ter). Differences in non-decision time had the opposite direction in controls and patients with frontal lesions. Patients with temporal lesions did not show a reliable difference between related and unrelated conditions.

temporal or frontal regions. Participants performed a word-picture matching task, in which they had to correctly verify whether congruent, semantically related and unrelated words matched pictures.

From the analysis of behavioral data, we found a semantic interference effect in RTs and errors for both patients and controls: related word-picture pairs resulted in longer RTs and more errors compared to the unrelated pairs. Patients on average had a higher error rate than control subjects. We note that the congruent condition is necessarily included in this task in order to give participants a task. However, we focused on the semantic interference effect, given that it better enables the study of semantic control. As we mentioned earlier, behavioral data alone does not allow exploring the nature - executive or/and semantic - of semantic interference. Therefore, we used a combination of RTs and accuracy to better understand latent cognitive processes underlying the process of semantic competition in the word-picture paradigm. We found that, for control participants, no reliable differences existed in drift rate between related versus unrelated word-picture pairs, whereas for both patient groups, an increased drift rate was found for unrelated in comparison to related word-picture pairs. Regarding the decision threshold, whereas controls had a higher decision threshold for related as opposed to unrelated conditions, the patients showed a lower decision threshold for related relative to unrelated word-picture pairs.

We formalized the process of lexico-semantic selection via a computational model of binary decision making, DDM, which provides an account of the process of lexico-semantic competition and resolution in terms of evidence accumulation (Anders et al., 2015; Ratcliff et al., 2004a,b). Previous studies related to the investigation of competitive lexico-semantic selection in both comprehension and production (Anders et al., 2017; Voss et al., 2013a,b) have shown that the process of lexico-semantic selection can be sufficiently described with two parameter types – the rate of evidence accumulation (drift rate) and the amount of evidence accumulation (decision threshold). While the drift rate can reflect the process of spreading activation (Gomez et al., 2013; Kinoshita et al., 2017; Voss et al., 2013a,b), the decision threshold reflects broad control mechanisms (Anders et al., 2017). We found that, for healthy controls, task demands in word-picture matching tap more into control mechanisms, rather than into the process of spreading activation through the lexical-semantic system. We also found that patients with temporal and frontal lesions have similar cognitive profiles with respect to mechanisms of control and spreading activation described by the drift rate and decision threshold, as established by the model.

Control participants. The mechanisms of lexico-semantic competition are usually discussed in terms of lexical activation and lexical selection when there is the need to map semantic features to lexical items or vice versa (Dell et al., 1997; Levelt et al., 1999; Roelofs, 1992). While the process of activation has been quite extensively studied (Dell et al.,

1997), the mechanisms of selection are still debated. According to many models of word production (Howard et al., 2006; Oppenheim et al., 2010; Roelofs, 2018), semantic features from several competing representations trigger the spreading activation in the semantic network, with the item with the highest activation level as a winner. It is plausible that the selection step requires executive control, especially in light of recent evidence dissociating activation and selection processes neurally (Piai et al., 2014). In the present study, we showed that in the context of lexico-semantic competition following the comprehension of spoken words, both high- and low competition conditions (related and unrelated word-target pairs) preserved the same level of activation in the semantic memory network (i.e., drift rate). Importantly, we showed that the selection of competing representations was supported by other mechanism potentially associated with executive control (i.e., decision threshold). This suggests that the mechanisms of semantic activation and selection may be dissociable (Nozari, 2017; Piai et al., 2014). Indeed, neuroimaging and lesion-based studies suggest that semantic selection (or control) and mechanisms of representation involve different brain areas (Jefferies, 2013; Lambon Ralph et al., 2017).

As for the "representation system", it is generally assumed that the anterior temporal lobes are crucial for representing semantic knowledge (Patterson et al., 2007), and damage to these areas due to, for example, degeneration leads to the degradation of semantic representations (Guo et al., 2013; Lambon Ralph and Patterson, 2008). Among the brain areas associated with the control of semantic retrieval and selection are the left IFG and posterior MTG. Patients with damage in these areas show poor results in face of semantic distractors, retrieve irrelevant information for the task, and are helped by cues when retrieving information (Jefferies et al., 2008; Jefferies and Lambon Ralph, 2006; Thompson-Schill et al., 2002). In addition, a recent neuroimaging meta-analysis study showed that left IFG and posterior MTG are consistently activated in many tasks designed to tap semantic control (Noonan et al., 2013). In the present study, we do not consider the drift rate measures to necessarily reflect the "representation system". In fact, none of our patients had semantic dementia, and some of the patients had both anterior and posterior parts of the left MTG damaged. Instead of indexing semantic knowledge per se, the drift rate may reflect the processes related to spreading activation in the lexico-semantic network. It is a common finding that the processes of lexico-semantic activation are tightly related to the left MTG (Baldo et al., 2013; Piai and Knight, 2018; Schwartz et al., 2009). By contrast, activity in frontal cortex is commonly interpreted as a control mechanism operating over lexico-semantic representations (Badre et al., 2005; Piai et al., 2014; Wagner et al., 2001). However the contribution of left IFG in the resolution of lexico-semantic competition still remains elusive (de Zubicaray et al., 2013; Piai et al., 2013, 2016; Piai and Knight, 2018; Python et al.,

2018). It is of importance to note that most of these studies address competitive word production. Studies investigating access to competing semantic representations using a word-picture matching task do not necessarily focus on the mechanisms of control per se but rather on the nature (lexical or semantic) of semantic interference (Campanella and Shallice, 2011; Harvey and Schnur, 2016). More broadly though, verbal comprehension mechanisms in both explicit (Demb et al., 1995; Spitzer et al., 1996) and implicit (Ruff et al., 2008) semantic tasks involve left IFG, which is associated with control mechanisms of semantic retrieval. Whether the function of control is deployed by IFG, posterior MTG, or a combination of both and in which contexts remains an open question. Below we discuss the mechanisms of semantic interference in an instance of competition for a comprehension task (word-picture matching) in patients with lesions overlapping in left MTG vs. left inferior and middle frontal gyrus.

Frontal patients. Previously it has been shown that patients with damage to the left PFC, and particularly left IFG, fail to appropriately adjust their decision threshold, in order to handle the increased task difficulty with a higher degree of semantic interference (Anders et al., 2017). The authors argued that their finding supports the idea that left PFC, and specifically left IFG, subserve an interference control mechanism, potentially similar across different cognitive domains (Kan and Thompson-Schill, 2004; Ries et al., 2014). In the current study, we showed that frontal patients (with most lesion overlap in left IFG and left MFG) perform differently in an interfering condition from healthy participants. While healthy participants adjusted only the decision threshold but not the drift rate, these patients showed abnormal modulations in both decision threshold and drift rate. When presented with a "high demands" condition (semantically related), patients with frontal lesions were slower and made more mistakes (lower decision threshold and lower drift rate) in comparison to the "low demands" condition (semantically unrelated), where they were faster and more accurate (higher decision threshold, higher drift rate). In other words, these patients were not able to easily solve semantic competition (low drift and threshold). This is in line with previous studies showing that patients with damaged frontal areas after a stroke had problems with controlled semantic retrieval in picture naming, as patients' responses were driven mostly by irrelevant associations (Humphreys and Forde, 2005; Jefferies and Lambon Ralph, 2006). It seems that patients with frontal damage are better at the less competitive condition (unrelated) because of still functioning (albeit abnormally) excitation levels in semantic and control systems, which is not the case for the more difficult (i.e. related) condition.

The fact that both activation and selection processes are jointly impaired in the patients with lesions in frontal areas suggests that there is a certain degree of interaction between these processes (Nozari, 2017). For example, depending on the task, selection processes resolve competing representations either by adjusting the selection criteria dynamically from the activation levels of the lexico-semantic system or by adjusting the criterion post-hoc, after a certain level of activation in the lexico-semantic system has been reached (Nozari and Hepner, 2018). It may be that the overlap between activation and selection processes depends on the language modality (production vs comprehension), which is an important variable to account for when comparing lexico-semantic competition in word-picture interference paradigms.

Temporal patients. For temporal patients, we expected the manifestation of the deficit at the level of activation in the semantic network, leaving the selection processes critically impaired as a result of deficiency of spreading activation. We indeed found that patients with damage to the left MTG were critically impaired in both decision threshold and drift rate mechanisms, which we interpret as deteriorated levels of semantic network activation and executive components operating on those representations. Interestingly, the pattern for both drift rate and decision threshold followed the same direction (increased for unrelated in comparison to related conditions), in line with the findings of the frontal patients, which suggests an interaction between processes

of semantic section and control.

Of note, the interpretation of the abovementioned results is highly dependent on the assumption that left posterior MTG contributes to lexico-semantic representations. However, the function of left posterior MTG remains somewhat elusive. Some studies propose that posterior MTG is a "knowledge hub" that links the associations between several concepts (Chao et al., 1999; Martin, 2007); other studies support the idea that posterior MTG participates in the control of semantic representations during retrieval (Davey et al., 2016; Noonan et al., 2013). A recent TMS study showed that left IFG and posterior MTG are crucial for semantic control rather than for semantic representation. Particularly, the study showed that these brain areas work in concert with each other, therefore the damage to either of these areas leads to disrupted manipulation of semantic knowledge (Whitney, Kirk, O'Sullivan, Lambon Ralph and Jefferies, 2011). Similar executive malfunctioning in semantic retrieval tasks in patients with temporal and frontal lesions is in line with previous evidence revealing functional connections between IFG and temporal areas (Bourguignon, 2014; Grappe et al., 2018). Taking into consideration these recent results with regards to the contribution of the posterior MTG to the processes of retrieval of semantic information, we could conclude that posterior MTG contributes not only to the drift rate but also to the decision threshold.

5.1. Limitations

It is of course essential to pinpoint that lesions vary across the patients in our sample (even with the same focal damage), and the patients in our study have more than posterior MTG of PFC lesions, for example including the superior temporal gyrus (STG) and parietal regions.

Previously, it has been shown that temporo-parietal lesions can lead to deficits in semantic control (Jefferies and Lambon Ralph, 2006). Some patients in this study had lesions in three parietal brain regions: post-central gyrus, supramarginal gyrus and inferior parietal gyrus. While to our knowledge there is no evidence that postcentral gyrus is involved in controlled semantic cognition, supramarginal gyrus and inferior parietal gyrus are thought to be part of the semantic cognition system. In the semantic control literature, parietal contributions (supramarginal gyrus and inferior parietal gyrus among others) are discussed in the context of temporo-parietal vs. prefrontal deficits. For example, persons with semantic aphasia, whose lesions are located not only in prefrontal cortex but also in temporo-parietal cortex manifested difficulties with controlling semantic representations (Jefferies and Lambon Ralph, 2006; Noonan et al., 2010, 2013). On the other hand, patients with inferior parietal or posterior temporal lesions did not exhibit impaired control over semantic activation in word production in comparison to patients with lesions in frontal cortex (Schnur et al., 2009). When it comes to the supramarginal gyrus, the evidence is not conclusive either. While there are studies showing the involvement of supramarginal gyrus in semantic control (Gennari et al., 2007; Nagel et al., 2008), a meta-analysis by Noonan et al. (2013) did not show significant activations in supramarginal gyrus, but rather within dorsal and anterior portions of angular gyrus, bordering the supramarginal gyrus. We inspected this issue in additional analyses after excluding patients with parietal lesions in the frontal group to capitalize on the distinction between temporo-parietal vs. frontal lesions (reported in Supp. Table 2 and Supp. Figure 2). Experimental effects remained unchanged (i.e., higher decision threshold and drift rate for the unrelated in comparison to related condition), which makes an explanation in terms of parietal lesions alone driving the effects less likely. Altogether, given the somewhat unclear evidence with respect to the contribution of supramarginal gyrus and/or inferior parietal gyrus to semantic control, we interpret our results with caution regarding this issue.

It is important to note that two frontal patients have additional lesions in the STG. It has been suggested that the STG among other regions is associated with semantic representations rather than with control processes (Noonan et al., 2013). Thus, the PFC group might have shown

additional disturbances in the lexico-semantic system (drift rate) in addition to the disturbed control exerted by the PFC (decision threshold). However, an additional analysis, which accounted for parietal contributions to the frontal group (see Supp. Table 2 and Supp. Figure 2), also excluded from the frontal group one patient with a large lesion in the STG. This additional analysis removed potential contributions of damage to the representation system from the frontal patients group. As reported above, experimental effects remained unchanged, which makes an explanation in terms of STG lesions contributing to our findings less likely.

Despite these control analyses, future studies, for example involving techniques such as TMS, are needed to explore the functional role of posterior MTG and left IFG in the context of degraded semantic retrieval with the modelling approach proposed here. Another limitation of the current study is that we cannot disentangle the contribution of the posterior and anterior portions of the MTG to the function of semantic control. Therefore, we cannot fully differentiate the contributions of control and representations to the process of semantic conflict resolution. Further studies should account for more precise differentiation of the lesions in order to clarify the function of semantic control in competitive selection in comprehension.

6. Conclusion

To conclude, we investigated the cognitive mechanisms of semantic interference in healthy subjects and patients with lesions overlapping in left MTG vs. left IFG/left MFG. We found that the driving force behind semantic interference in word-picture matching in healthy subjects lies in the domain of executive control, rather than at the level of spreading activation in the lexico-semantic system. Patients with temporal and frontal lesions showed a similar pattern in the underlying mechanisms of semantic control in the context of word-picture matching, which suggests similar functional contributions of the posterior MTG and IFG to semantic competition during retrieval. These results support the notion that activation and selection are distinct but interactive processes that have to be preserved in order to resolve semantic interference efficiently.

Data availability

The datasets for this study and analysis scripts are available on the Open Science Framework (OSF) https://osf.io/9jqxn/.

CRediT authorship contribution statement

Lara Todorova: Conceptualization, Formal analysis, Visualization, Data curation, Writing - original draft, Writing - review & editing. **David A. Neville:** Formal analysis, Writing - review & editing. **Vitória Piai:** Conceptualization, Data curation, Writing - review & editing.

Acknowledgements

The authors are grateful for the patients and their families, as well as for the other volunteer participants for taking part in this study. We would like to thank Donatella Scabini and Brian Curran for patient delineation, Brian Curran, Clay Clayworth, and Callum Dewar for lesion reconstruction, and the members of the Center for Aphasia and Related Disorders at the VAHCS in Martinez, CA, for neuropsychological testing. The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2020.107560.

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