A concise overview of the spatial and temporal underpinnings of lexical selection in spoken word production

Vitória Piai* and Arushi Garg
Radboud University, Donders Centre for Cognition, Thomas van Aquinostraat, 4, 6526 GD, Nijmegen, the Netherlands

Vitória Piai*: vitoria.piai@donders.ru.nl, corresponding author
Arushi Garg: arushi.garg@donders.ru.nl

Abstract

Word production and comprehension both require mapping between the meaning, form, and syntactical representations of the word. We refer to the collective set of processes involved in performing this mapping as lexical selection. In the field of word production research, how lexical selection is carried out in the brain is studied using many different methods (e.g., brain imaging with spatial or spatio-temporal resolution, brain stimulation, lesion-symptom mapping), different tasks (different kinds of naming and control tasks), and different experimental paradigms or manipulations (e.g., picture-word interference, blocked-cyclic naming, continuous naming). In this chapter, we bring together evidence from different word production studies to summarise our current understanding of the spatial and temporal underpinnings of lexical selection.

Keywords

Aphasia; Brain stimulation; Electrophysiology; Lesion-symptom mapping; Lexical selection; Naming; Neuroimaging; Semantic context effects; Speech; Temporal lobe; Word production;

Key points/objectives

- Define lexical selection generally, in a theory-neutral manner
- Briefly review methods, tasks and paradigms used to study lexical selection
- Review evidence for spatial localisation of lexical selection: neuroimaging (fMRI, NIRS), lesion-symptom mapping, non-invasive and invasive brain stimulation
- Review evidence for spatially informed time course of lexical selection: electrophysiology (scalp and intracranial EEG, MEG), chronometric non-invasive brain stimulation
- Review spatial and spatio-temporal evidence from studies looking at semantic context effects

Conflict of interest disclosure

The authors do not have any conflict of interest to disclose

1. Introduction

We spend a large part of our lives producing and understanding language. Words are at the core of these activities. This article focuses on what we know about what goes on in our brains when we choose what words to produce. More specifically, this article is about *lexical selection*. We start with a definition of lexical selection that is relatively theory-neutral and that will guide the remainder of this article.

Here, we define lexical selection as the set of processes that occur during meaning to sound (in production) or sound to meaning (in comprehension) mapping, specifically in selecting representations that are associated with whole words - concept/meaning (e.g., lexical concepts), form representation of the word (morpho-phonological), lexical or syntactic representations (e.g., lemmas, syntactic frames) or any other representations in between. For word production, this represents the processes from, and including, the activation of the target lexical concept until, and including, the selection of the target morpho-phonological representation.

1.1. Common paradigms tapping into lexical selection

Different paradigms have been used in the literature to tap into lexical selection for word production, both behaviourally and neurally. From these (also in combination with an experimental manipulation), researchers can derive response latencies, amount of errors made, or the types of errors made. Neurally, these (experimental) effects can be related to changes in brain activity or to patterns in brain pathology. Below, we briefly discuss some widely used paradigms that will form the basis for interpreting the neural findings we focus on in this article.

The most basic of word production tasks are naming tasks in which each trial occurs without any additional manipulations. In a simple picture naming paradigm, participants are presented with pictures of objects one by one and are asked to name them. The picture stands for the concept for which a speaker selects a word (lexical item). In auditory naming (also called ‘naming to definition’), participants are required to respond with a word when presented with its definition (e.g., “What a king wears on his head”). This type of naming differs from visually guided (“picture”) naming with respect to the lead-in process but should, nevertheless, remain comparable to picture naming after the initial modality-specific processes. This is to say that conceptual and lexical selection should overlap between the two forms of naming. In contextually guided naming, a sentence is presented with the target word omitted, which is then presented as a picture for participants to name (e.g., “The farmer milked the”, followed by the picture of a cow). Alternatively, connected speech or (semi-)spontaneous production can be elicited via picture description, interviews, etc., and researchers can examine words, sentences, discourse, etc.

Of note, these tasks in themselves do not easily isolate the lexical selection stage. For that, one needs to go beyond just the task itself. For example, researchers can examine how linguistic properties of the picture names or words produced affect naming times or errors: Variables such as the frequency of a word’s usage have been argued to tap into the lexical selection and word-form retrieval stages (e.g., Almeida et al., 2007; Kittredge et al., 2008; see also Jescheniak & Levelt, 1994). Words used less frequently (or acquired later) are produced more slowly and are more prone to errors.

The types of errors produced can also be linked to different stages of word production. Here, we focus on a few types of errors related to conceptual and lexical selection. Semantic errors, such as saying "oven" instead of the (pictured) concept FRIDGE, are thought to originate at the conceptual or lexical stages, that is, a speaker may have selected the incorrect concept, or the incorrect lexical item associated with that concept (Dell et al., 1997). In cases of word-finding problems such as anomia, tip-of-the-tongue states (TOT), or omission errors, a speaker has accessed conceptual information, but only partial phonological information is available. These errors or difficulties are thought to tap into lexical selection (e.g., Dell et al., 2004). Thus, in the remainder, we will focus on these types of errors or difficulties as indexing the lexical selection stage. We will use the following distinction throughout: The term 'anomia' will be reserved for cases when a participant is able to utter speech, just not the picture name (e.g., "This is a…" but no label, or "I know it"), whereas 'omission errors' will be reserved for cases when the task is to name a picture but no response is given.

1.1.1. Semantic-context effects

Experimental manipulations can be added to picture naming, allowing researchers to better isolate the lexical selection stage. We will focus on three different approaches, all making use of so-called semantic context effects. Although there has been heated debate in the field, there is general agreement that this type of semantic context effect taps into lexical selection (Roelofs, 2018).

In picture-word interference, a picture is presented together with a distractor word, presented auditorily or visually (Glaser & Düngelhoff, 1984; Lupker & Katz, 1981; Rosinski, 1977; Schriefers et al., 1990). If the picture and the distractor are semantically related by belonging to a same category (e.g., pictured GOAT, distractor "mouse", both animals), people are slower and more error-prone to name the pictures compared to unrelated distractors (e.g., distractor "chair"). This effect has been argued to arise during lexical selection (Roelofs, 1992).

To an uninformed participant, the continuous naming paradigm is similar to a simple picture naming task. The participant sees only one picture at a time and needs to name it. The manipulation is introduced in the order in which pictures are presented. Pictures from a semantic category are mixed together with pictures from other categories and are separated from other pictures of the same category by a minimum of two pictures from other categories. Presented this way, each successive picture from a semantic category is found to be named slower than its predecessor from the same category resulting in cumulative semantic interference effects (Howard et al., 2006).

In blocked-cyclic naming, participants name pictures in blocks. There are two types of blocks: homogeneous and heterogeneous (Damian et al., 2001). In homogeneous blocks, the pictures presented are all from the same semantic category (e.g., five consecutive pictures of animals are shown), while in heterogeneous blocks, the pictures belong to different semantic categories (drawn by mixing the items presented in the homogeneous blocks, e.g., five pictures each from a different category). Participants cycle over the different blocks. From the second cycle onwards, picture naming is slower and more error prone in homogeneous blocks relative to heterogeneous blocks.

There has been much discussion in the psycholinguistics field about semantic-context effects in word production (Nozari & Pinet, 2020; Roelofs, 2018; Roelofs et al., 2013). However, we would argue that these views differ at a more fine-grained level of definition of the different cognitive stages involved in lexical selection, whereas under the broad definition we provided above, almost all views would be compatible with semantic-context effects providing a window into lexical selection in word production.

1.2. Common neural methods

Among the commonly used methods to study neural activity corresponding to lexical selection, we will cover (scalp and intracranial) electrophysiology, functional magnetic resonance imaging (fMRI) based on blood oxygen-level dependent (BOLD) contrast, non-invasive and invasive brain stimulation, and lesion-symptom mapping. We refer the reader to additional literature for an explanation of these methods. Importantly, all neural methods have their caveats. Therefore, we will focus on converging evidence across different methods.

Some methods allow us to measure brain function while we select words. Here, we will focus on two of these methods. Electrophysiological methods (both electro- and magnetoencephalography, EEG and MEG) measure the electrical activity of neurons or the magnetic fields generated by this electrical activity. EEG signals can also be recorded intracranially (iEEG) in neurosurgical cases (Flinker et al., 2018). These methods provide information about the time course of activity in different brain areas. BOLD fMRI provides an indirect measure of brain activity by imaging oxygen consumption related to neural activity. A related technique, near-infrared spectroscopy (NIRS), also provides a measure derived from the brain’s hemodynamics and has similar properties as BOLD fMRI.

Other, so-called stimulation, methods transiently modulate brain function. A targeted brain area is stimulated, thereby increasing or decreasing its activity, and one measures the effect this has on behaviour, such as the types of errors made during picture naming, or the response latencies. Stimulation can be applied on the scalp (i.e., non-invasively) using transcranial magnetic stimulation (TMS) or directly onto the cortex (i.e., invasively) using direct electrical stimulation (DES) in neurosurgical patients to identify critical areas that should be preserved.

Finally, an approach that combines information about brain structure and behavioural measures is lesion-symptom mapping. With this approach, the relationship between locations of brain damage and language performance measures are mapped statistically (de Haan & Karnath, 2018).

In general, certain methods provide only spatial information, other methods temporal information only, and other methods a mixture of both. When discussing the literature, we will highlight the type of relevance contributed by the different methods.

2. Evidence from Neural Methods

2.1. Spatial dimension

In the following sections, we will discuss the evidence across various methodologies that provide information in particular about the spatial dimension, that is, which brain areas have been associated with lexical selection (i.e., fMRI, NIRS, DES, TMS, and structural MRI-based measures such as lesion-symptom mapping).

2.1.1. Errors in simple naming and variables in naming and connected speech: evidence from fMRI and lesion-symptom mapping

Volfart et al. (2022) is perhaps the only study examining different error types made by neurologically intact participants in a picture naming task using neural measures (fMRI, in this case). Amongst the speech errors examined were semantic and omission errors. When comparing trials with semantic errors to trials with correct responses to the same pictures, perfusion signal changes (decreases, in particular) were found in the left posterior middle temporal gyrus (MTG) and left angular gyrus. Omission errors did not yield significant differences relative to matched correct responses.

Schwartz and colleagues conducted voxel-level lesion-symptom mapping (VLSM) studies focused on semantic errors during picture naming in a sample of people with aphasia due to stroke (Schwartz et al., 2009; see also Walker et al., 2011). These authors found that the production of semantic errors during picture naming was mostly associated with lesions in the (mid portion of) the MTG, in addition to a smaller cluster in left lateral prefrontal cortex. After correcting for verbal and nonverbal comprehension errors, the strongest associations remained within the left temporal lobe.

Stark et al. (2019) also focused on semantic errors in stroke-aphasia. The errors were produced during connected speech elicited by a picture description task. Posterior superior temporal gyrus (STG) and MTG were the areas that were most strongly associated with semantic errors. These authors additionally reported semantic errors during picture naming in a different group of participants with stroke-aphasia. Here, too, semantic errors were mostly associated with lesions to the left posterior STG, MTG, and inferior temporal gyrus (ITG).

Omission errors in stroke-aphasia during picture naming have also been examined (Chen et al., 2019). These authors found two different clusters of regions associated with omission errors: one in the left middle and inferior frontal gyri, and one in the mid and anterior portions of the left MTG and temporal pole.

Besides specific types of errors, global picture naming accuracy has also been used in combination with VLSM. Baldo et al. (2013) examined picture naming accuracy in a stroke-aphasia sample while covarying for visual perception and overall speech fluency deficits. These authors found that mid and posterior portions of the left MTG were the most strongly associated with deficits in picture naming. Due to using a global picture naming score measure, these results cannot be as directly related to word production stages as semantic or anomic/omission errors. Yet, they converge with the findings previously described in terms of the importance of the left temporal lobe for picture naming.

In an attempt to summarise the stroke-aphasia VLSM literature, Piai & Eikelboom (2023) conducted a systematic review and meta-analysis of picture naming VLSM studies reporting on unique, non-overlapping cohorts. Ten papers were included that did not distinguish the types of errors, but instead looked at global naming scores. The meta-analysis indicated two clusters, one predominantly in the anterior portion of the left temporal lobe, including STG, MTG, and ITG, and the other predominantly in the posterior portion of the left temporal lobe. However, these findings suffer from the same issue that global accuracy scores cannot be readily related to any stage in word production. Therefore, Piai & Eikelboom (2023) also examined five studies with unique groups of participants reporting on measures that more directly map onto conceptual and lexical selection. They concluded that deficits in conceptual-lexical selection stages tend to be associated with lesions in mid to posterior left temporal lobe regions.

Most of the literature on speech errors following brain pathology focuses on stroke-aphasia, but converging evidence is found when one examines other pathologies, which we review next.

In a VLSM study examining individuals with brain tumours, semantic errors and omissions in picture naming were analysed together (Faulkner & Wilshire, 2020). These errors were found to be associated with tumours in posterior MTG and ITG, and in the posterior fusiform gyrus. Isella et al. (2020) examined relationships between semantic errors in picture naming and areas of hypometabolism in individuals with Alzheimer disease. Again, semantic errors were associated with the mid portion of the MTG and left ITG.

Wilson et al. (2010) studied a group of individuals with primary progressive aphasia, a type of fronto-temporal dementia. The authors examined the relationship between atrophy and the production of nouns of increasing lexical frequency (a proxy for easier lexical selection) in continuous speech. They found associations predominantly in the mid portion of the left temporal lobe (mainly in the MTG) and in the fusiform gyrus. Bruffaerts et al. (2020) also examined atrophy in a sample of primary progressive aphasia, in their case in relation to errors or difficulties in picture naming. Left-hemisphere atrophy in the mid and posterior portions of the fusiform gyrus, posterior MTG and ITG, among other occipital and frontal regions, was found to be related to the percentage of semantic errors produced by the patients. For omissions, correlated atrophy was found in left and right medial anterior temporal lobe with a posterior extension encompassing perirhinal and parahippocampal areas, and right angular gyrus. The clusters of regions related to semantic errors and omissions did not overlap, and no relations were found between atrophy and percentage of semantic errors or omissions in a sample of matched controls.

Binder et al. (2020) used VLSM to examine regions related to picture naming decline after epilepsy surgery in a sample of 59 individuals, all having surgeries to the left temporal lobe. Picture naming decline was associated with resections or ablations of the mid portion of the left fusiform gyrus (between Talairach y = -15 to y = -35) and adjacent inferior temporal gyrus.

The frequency effect in picture naming, associated with lexical selection and word-form retrieval, has been examined by Graves et al. (2007) taking into consideration object familiarity and word length. Only one area in the mid portion of the left STG was found to be modulated by the frequency of the target picture name, with increases in activity for increasingly lower frequencies.

In sum, based on findings from errors in spoken word production or from other variables that likely tap into lexical selection, the literature converges on a locus in the temporal lobe, with a prominence for the middle temporal gyrus and inferior temporal gyrus (and adjacent fusiform gyrus).

2.1.2. Errors in naming: Evidence from direct electrical stimulation

A number of studies have been published over the years with an increasingly larger number of participants undergoing DES. Here, we highlight some relevant ones given their reports on anomia and semantic paraphasias within the same cohort of patients. See also Chang et al. (2017) for a large sample study reporting on omission errors, not discussed below because semantic errors and anomias/omissions were not reported together for the same sample.

Corina et al. (2010) reported 36 cases undergoing DES either for intractable epilepsy or tumor surgery. Semantic errors were found predominantly in the left hemisphere in the middle portion of the post-central gyrus, the anterior supramarginal gyrus (SMG), and the posterior MTG. Omissions were less readily interpretable given an uneven distribution across patients. Nevertheless, prominent sites in the left hemisphere resulting in omissions were the middle portion of the pre-central gyrus and post-central gyrus, the angular gyrus, and posterior MTG.

Miozzo et al. (2017) reported 68 epilepsy cases undergoing DES. Semantic errors and omissions were analysed both as a function of gyrus within the left temporal lobe as well as the portion within the temporal lobe in the anterior-posterior direction. Semantic errors were more prominent when the left MTG was stimulated relative to the other gyri, whereas omissions were more prominent in the ITG relative to other gyri. With regards to the relative localisation of effects within the temporal lobe, semantic errors were more common when the mid portion of the left temporal lobe was stimulated, while omissions were more common when stimulations happened relatively more anteriorly.

Sarubbo et al. (2020) reported 256 cases undergoing DES for brain tumour surgery. Semantic errors were associated with stimulation of the left mid and posterior STG and MTG (and right STG), and left middle and inferior frontal gyri, and anomias were associated predominantly with stimulation in the left STG, MTG and ITG.

Tate et al. (2014) also used a large cohort of 165 brain tumour cases to derive probability maps of semantic errors and anomias. The highest rates of anomia were found in the left hemisphere in the STG, SMG, and MTG. Semantic errors showed a more distributed pattern in the left hemisphere, with the most prominent clusters at the junction of posterior STG and SMG, in the inferior frontal gyrus (pars triangularis and opercularis), and in dorsal premotor cortex.

Interestingly, when semantic paraphasias were further split into different types of errors depending on their relationship in meaning with the target word, co-hyponym errors (i.e., members of a same semantic category, e.g., saying “apple” instead of “pear”, both being fruit) were associated with the left temporal lobe, and in particular the MTG (Gobbo et al., 2021). By contrast, the production of synonyms (e.g., saying “telly” instead of “television”) was associated with left IFG.

One DES study relevant for the topic of lexical selection despite the smaller sample (9 patients, all with left hemisphere DES mapping) was conducted by Vidorreta et al. (2011). When naming pictures with a lead-in sentence to test for anomia (e.g., “This is…”) in languages that have gender marking for nouns, the determiner has to be produced with the correct (syntactic) gender. According to theories of spoken word production, gender or, in general, syntactic information about a word becomes available during lexical selection and before form information about the word can be accessed (e.g., Dell & O’Seaghdha, 1992; Levelt et al., 1999). In the study by Vidorreta et al. (2011) conducted in French, errors in the selection of the correct determiner were identified (e.g., “Ceci est un pipe” instead of “une pipe”). In 3/9 cases, these errors were produced with stimulation of the left IFG and in 3/9 cases with stimulation of the posterior portion of the MTG. Interestingly, naming errors were not elicited with stimulation of these sites in these individuals, suggesting a process that takes place during lexical selection but might not be crucial for it.

2.1.3. Errors in naming: Evidence from TMS

An approach using TMS consists of stimulating multiple brain areas by moving the coil over the head, yielding maps of errors associated with stimulation to different regions. One study, for example, found semantic errors in the left hemisphere elicited most prominently following stimulation of the posterior middle frontal gyrus, anterior supramarginal gyrus, and ventral postcentral gyrus. Right-hemisphere stimulation, in turn, led to more semantic errors when applied to the mid and posterior portions of the STG and anterior supramarginal gyrus (Sollmann et al., 2015). Omissions are relatively more common than semantic errors. For example, Krieg et al. (2016) found that between 5.2% and 5.8% of the left-hemisphere stimulations in their study resulted in omissions. The authors split their analyses into male and female participants and found that 33% of those omission errors in males were associated with posterior MTG stimulation, followed by other temporal lobe sites, namely in the STG and MTG (between 8% and 9%). In females, by contrast, the pattern was different, with no prominent site standing out much above the others, unlike the pattern in the male participants: between 7% and 8% of the omissions were elicited by ventral postcentral gyrus, anterior STG and anterior SMG, and pars opercularis of the IFG. Omissions were also commonly elicited after stimulation of left ventral precentral gyrus and pars opercularis of the left IFG in the study by Sollmann et al. (2017) at multiple values of the time interval between the picture onset and the onset of the TMS pulse (varying from 0 ms, i.e., simultaneously, to 500 ms). We refer the reader to Ohlerth et al. (2021) for a comparison between object picture naming and action picture naming.

2.1.4. Comparisons between different types of naming

A number of studies used the logic of comparing visually guided naming with some other form of naming (auditory or contextually guided) to highlight overlapping areas relevant for word production regardless of the lead-in process to evoke the concept.

For example, Hamberger et al. (2001) compared the effect of DES on both visual and auditory naming in different regions of the left, language-dominant temporal lobe. Whereas anterior temporal lobe stimulation (< 4 cm from the temporal pole) disrupted auditory naming only, posterior temporal lobe stimulation (> 4 cm from the temporal pole) disrupted both visual and auditory naming.

Roos et al. (2023) used fMRI in neurologically healthy participants and compared areas overlapping between contextually guided naming and visually guided naming. Participants were presented with sentences that were missing the final word, which was represented by the picture to be named by the participant. There were two conditions: constrained and unconstrained naming (see Figure 1). The word (or picture) is contextually cued by the sentence in the constrained condition but not in the unconstrained condition. The moment of lexical selection (in addition to other stages) was assumed to be different per condition: during the interval prior to picture presentation for the constrained trials (contextually guided retrieval) and at picture presentation for unconstrained trials (visually guided retrieval). Areas were identified where the BOLD signal increased prior to picture presentation for constrained > unconstrained trials as well as at picture presentation for unconstrained > constrained. These overlapping areas, shown in purple in Figure 1, were the mid and posterior portions of the left MTG, the left fusiform gyrus, and the pars triangularis of the left inferior frontal gyrus.

Forseth et al. (2018) used iEEG and DES in a paradigm in which they used a visual and an auditory control task in addition to visual and auditory naming tasks. Participants saw scrambled images and had to respond by saying “scrambled” (a low-level control task for visual naming) or they heard temporally reversed sentences and had to respond verbally whether the voice was male or female (a low-level control task for auditory naming). Here, we discuss their analyses on the conjunction between visual and auditory naming. For the iEEG data, focusing on the broadband gamma signal (a global indicator of local, cortical activity) in the 1 second prior to naming onset, areas were identified where auditory naming was different from a low-level control reversed speech condition, *and* picture naming was different from a low-level control scrambled images condition (“conjunction analysis”). These left-hemisphere areas were the middle fusiform gyrus, intraparietal sulcus, supplementary motor area, and IFG. In this analysis, the posterior portion of the left MTG was not identified in the conjunction analysis as it was uniquely present in the auditory naming versus reversed speech contrast only. For the direct cortical stimulation analyses, areas were identified where stimulation disrupted picture naming *and* naming to definition, while not disrupting sentence repetition nor affecting movement or sensation. Two sites were identified with these properties: the mid portion of the left fusiform gyrus and the posterior portion of the left MTG.

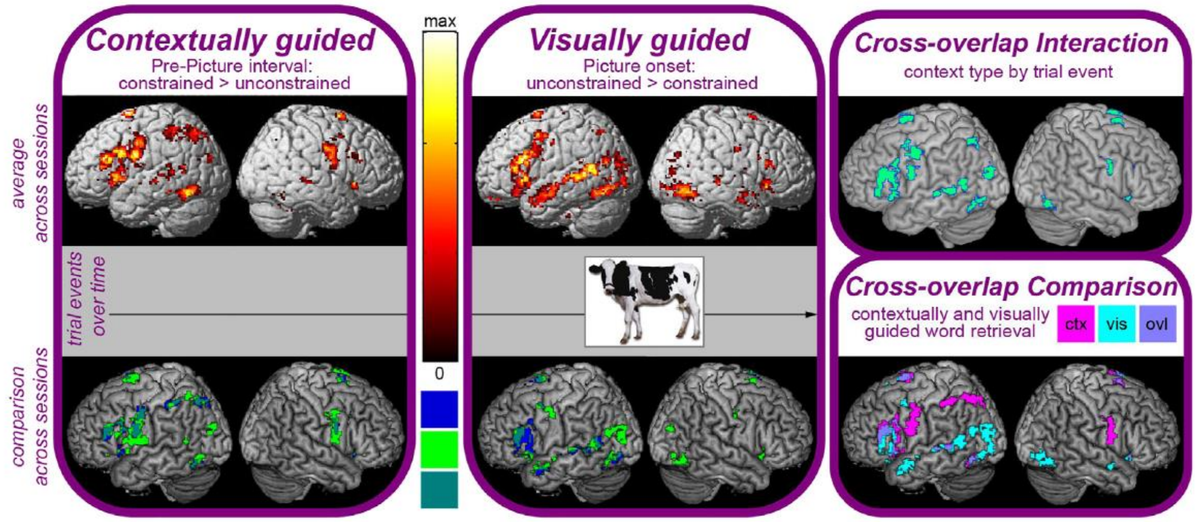

Figure 1. Top row: T-contrasts of BOLD increases for constrained over unconstrained contexts at the pre-picture interval (left column), and unconstrained over constrained contexts at the picture appearance (middle column), averaged across sessions. Bottom row: session consistency of differences between contexts (i.e., of contrasts presented in top row). Dark blue = Session 1, green = Session 2, teal = common to both sessions. Right column, top: interaction between context type and trial event (i.e., pre-picture interval vs picture appearance). Right column, bottom: cross-overlap of contextually and visually guided word retrieval. Pink = contextually guided, cyan = visually guided, purple = common to both ways of word retrieval. All clusters are significant on cluster level, FWE-corrected P < .05. Reproduced with permission granted by N. M. Roos, A. Takashima, and V. Piai from https://doi.org/10.17605/OSF.IO/2FVGB. No changes were made.

In sum, comparisons between visually guided picture naming versus other forms of naming (auditory or contextually guided) converge on posterior left temporal lobe (and in particular MTG). It remains the case that the overlap between visual and auditory or contextually guided naming happens at more stages (e.g., syllabification, phonetic encoding, articulation) than just conceptual and lexical, thus these types of comparisons do not uniquely isolate the lexical selection stage. Nevertheless, some of the sites found in these comparisons (i.e., visual vs auditory or contextually) do converge with the literature we have reviewed so far in other sections.

2.1.5. Interim conclusion on spatial dimension

In summary, the most prominent areas found associated with lexical selection are in the left temporal lobe, in particular superior, middle, inferior temporal, and fusiform gyrus, in addition to left inferior frontal gyrus and, to a lesser extent, left supramarginal and angular gyrus. We note, however, that spatial information alone is not necessarily informative for understanding what lexical selection is or how it takes place. Nevertheless, studies that examined semantic errors and omissions/anomias within the same population and task (e.g., Bruffaerts et al., 2020; Miozzo et al., 2017; Sarubbo et al., 2020; Tate et al., 2014; Volfart et al., 2022) often find (somewhat) different underlying areas for these types of errors. Studies of this type could help refine theories of lexical selection by providing support to the view that different stages of lexical selection might be playing into semantic vs omission/anomic errors or, similarly, that some areas/ processes at play in one type of error might not be at play in the other.

Above, we have used a terminology for the division of gyri into anterior, mid, and posterior portions. Sometimes, this terminology was taken from the authors' own writing, sometimes it was our own division based on coordinates. These divisions in the literature are largely arbitrary and not based on anatomical markers or histology of the constituent cells. None of these divisions are consistently used in the literature. Therefore, the evidence reviewed above cannot, and should not, be used to make claims distinguishing the relative localisation of the processes implicated within a structure, i.e., we cannot lay claims to whether a process arises more anteriorly or posteriorly within a structure.

2.2. Spatio-temporal dimension

We now turn our attention to studies examining the time course of brain activity when related to brain regions identified in the previous sections. Time course data is often achieved through studies employing electrophysiology and chronometric TMS. In the case of electrophysiology, we will only look at studies utilising intracranial EEG or source reconstruction of scalp data (in the case of brain lesions, only if the source reconstruction took the lesion into account, see Piastra et al., 2022; van den Broek et al., 1998).

Edwards et al. (2010) reported individual participant data from an intracranial EEG study in which patients performed a picture naming task. In one of their patients, recordings were obtained via an electrode grid placed over the left temporal lobe. Given that these types of studies are conducted in individuals with epilepsy, it is important to ascertain that the recorded activity does not present signs of epilepsy, which was the case for the recordings from the left temporal lobe in this patient. The patient named the pictures with a median response time of 1026 ms. Activity in the posterior portion of the left MTG was at the level of the pre-picture baseline until about 350 ms post picture onset. Around this point in time, the activity in this area significantly increased above baseline levels and remained sustained until around 200 ms pre-response onset. By contrast, posterior STG showed no increases (if anything, even suppressed activity) beyond the baseline level of activity during the same period. Precentral gyrus sites showed significantly increased activity above the pre-stimulus baseline level starting around 550 ms prior to speech onset and remained sustained, similar to postcentral gyrus sites, but with a slight shift to a later latency.

In an MEG study by Liljeström et al. (2009) of picture naming, the authors reported a progression of increased activity beyond pre-stimulus baseline levels from early visual areas around 150 ms to the occipitotemporal cortex bilaterally around 220-240 ms and parietal cortex bilaterally around 300 ms. From around this point in time onwards, activity became more sustained (i.e., increased for longer periods of time beyond baseline levels) in the left posterior (and right superior) temporal cortex, followed finally by the frontal cortex bilaterally (for similar findings, see also Sörös et al., 2003; for comparisons across different tasks: Vihla et al., 2006).

Ala-Salomäki et al. (2021) examined the test-retest reliability of MEG-based measures in a picture naming study (although they used a delayed naming task), compared to a delayed control (visual) task (i.e., saying “yes” if the presented picture had a red cross in the middle). High consistency between two measurement days was obtained with the following pattern. Starting around 200 ms post stimulus onset, increased activity relative to the control task was found in left parietal (until around 600 ms) and left temporal and sensorimotor (until around 800 ms) sources. Left frontal and left occipital sources had a somewhat later time course, between 400-800 ms.

Using picture naming and MEG, Chupina et al. (2022) reported a single case of a young-adult stroke (patient J.) who presented with marked anomia. The patient was asked to indicate anomic states during task performance such that these could be differentiated from, for example, cases in which she could not recognise the picture. Successful naming trials (47% of total trials) were contrasted with anomic trials (42%), for which the largest difference in event-related fields amplitude occurred between 330 and 440 ms. Source localisation indicated that, within this time window, successful naming had stronger activity in the mid to posterior portions of the right temporal lobe relative to anomic trials, whereas anomic trials had stronger activity in the right IFG. These results are shown in Figure 2. The effects in this patient were found in the right hemisphere, most likely given the extent of the lesions in the left hemisphere (as discussed by Chupina et al., 2022). Interestingly, however, the relative areas within that hemisphere (i.e., mid-posterior portions of the temporal lobe, IFG) are highly comparable to the areas in the left hemisphere discussed so far.

Online chronometric TMS studies have been conducted probing different brain regions at particular time points to provide spatio-temporal evidence on spoken word production stages. Here, we focus on chronometric TMS studies probing the regions of interest in the left temporal lobe, given the prominence of this lobe in the evidence reviewed thus far.

Acheson et al. (2011) stimulated left mid-to-posterior MTG in a picture naming task and found that naming was slowed down with stimulation applied between -100 to 200 ms relative to picture onset as compared to a no-stimulation control condition. Schuhmann et al. (2012) compared stimulation of the left mid portion of the MTG, left posterior STG, and left IFG at five different time windows relative to picture onset (150, 225, 300, 400, and 500 ms) with a no-stimulation control condition. Stimulation to the mid portion of left MTG slowed down picture naming times at 225–275 ms and 400–450 ms relative to picture onset, whereas posterior left STG stimulation slowed down naming at 400–450 ms. Finally, left IFG stimulation slowed down naming at 300–350 ms. See also Sollmann et al. (2017) for a chronometric TMS study reporting on errors rather than naming latencies.

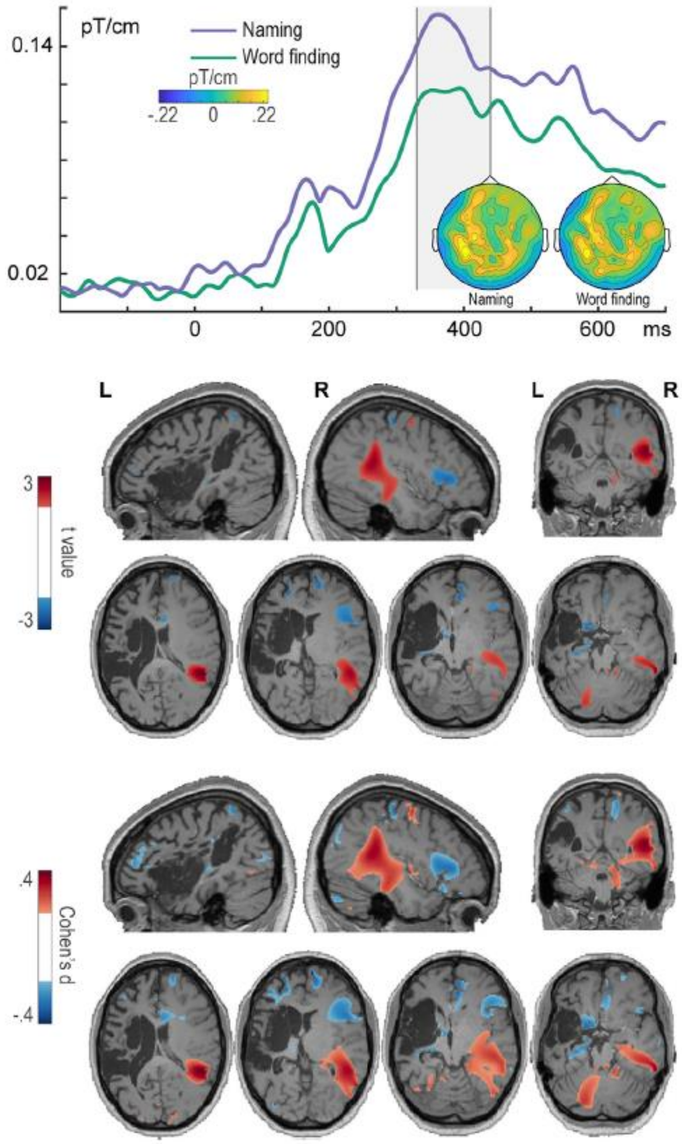

Figure 2. Event-related fields (ERFs) and sources of naming-related responses. (a) ERFs for J.'s naming (purple) and word-finding (green) trials (from planar gradients), averaged over posterior left and right sensors. The ERFs are displayed between −200 and 700 ms. The time window selected for the topographical maps and source analysis is indicated by the shaded area (identified by the cluster-based permutation analysis). For the source maps (b, c), values were thresholded at t values (b) more extreme than ±2 and Cohen's d (c) more extreme than ± 0.2 (white masks in the left colour bars). Positive values indicate stronger responses for naming relative to word-finding; negative values indicate stronger responses for word-finding relative to naming. Slices are depicted in neurological convention (i.e., left hemisphere on the left-hand side). L, left; R, right. Reproduced with permission from the authors from https://doi.org/10.6084/m9.figshare.19228194.v2. No changes were made.

Jodzio et al. (2023) conducted a modified replication of Schuhmann et al. (2012) and, importantly, the authors considered the impact of individual variability in naming times. Three different regions were probed: left posterior MTG, left posterior STG, and left IFG, all stimulated at 225, 300, 375, 450, or 525 ms relative to picture onset. The most consistent finding in that study was that left IFG stimulation affected picture naming times about 100 ms prior to speech onset. Left posterior MTG and STG stimulation, by contrast, also affected picture naming times but the effects were less clear-cut, with interference effects found for stimulation around 100 ms prior to speech onset and facilitation effects for stimulation applied around 225–350 ms relative to picture onset. Critically, when considering the impact of individual variability in naming times and the nonspecific effects of TMS, including muscle stimulation confounds, the authors provided a nuanced interpretation of findings from chronometric TMS studies.

In sum, the electrophysiological data indicates (left-lateralised or bilateral) temporal and parietal lobe involvement in a relatively early period following picture onset, *after* visual areas' and *before* frontal areas' engagement. The exact timing of lexical selection is difficult to derive, even if a study would be able to uniquely isolate the processes of interest, given the variability in speech onset latencies across trials, individuals, and studies (Piai, 2016). Nevertheless, across all evidence, parts of the temporal lobe (sometimes also labelled by authors as temporoparietal or occipitotemporal) seem to become involved starting around 200-300 ms after picture onset (see also Indefrey, 2011; Indefrey & Levelt, 2004). The evidence from TMS is weaker and cannot be taken to either unequivocally support or refute the spatio-temporal evidence from electrophysiology, but the little evidence available is somewhat in line with these timing estimates.

2.3. Semantic context effects

Previous reviews have summarised the spatial and temporal characteristics of semantic context effects (de Zubicaray, 2023; de Zubicaray & Piai, 2019; Nozari & Pinet, 2020). For example, de Zubicaray and Piai (2019) provided the first (semi-)systematic review of semantic context effects, separated by paradigm, namely picture-word interference, blocked-cyclic naming, and continuous naming (see also Nozari & Pinet, 2020, for a critical review of the literature on semantic context effects). Therefore, here we will mainly focus on discussing the main findings of these reviews, while adding information on more recent findings (since these reviews were completed) when relevant. In reviewing the more recent studies, we will focus on the brain areas identified in the sections above (mainly in the temporal lobe) and therefore we will give more prominence to spatial and spatio-temporal methods that provide additional anatomical information either from intracranial EEG or by means of source localisation.

2.3.1. Picture-word interference

In the case of picture word interference studies, the relevant contrast that can be used to study lexical selection is that between semantically related (more specifically, pertaining to the same semantic category) versus unrelated word distractors. Various fMRI studies and one MEG study have used this contrast, but as discussed by de Zubicaray and Piai (2019), many deviated from a more typical design, making comparisons across studies more difficult. Four fMRI studies and one MEG study (see Figure 3), all with relatively very similar designs (de Zubicaray et al., 2013; de Zubicaray & McMahon, 2009; Gauvin et al., 2021; Piai et al., 2013, 2014), provided converging spatial evidence that the semantic context effect (i.e., related vs unrelated picture-word interference conditions) is associated with activity differences in portions of the temporal lobe, and in particular left MTG and STG. Of note, the *direction* of the difference in terms of brain activity is not always aligned across studies, nor with the direction of behavioural effects, that is, both decreased and increased activity has been found when contrasting related to unrelated distractors, despite increased naming latencies for related vs unrelated conditions. The MEG study by Piai et al. (2014, Figure 3) provided spatio-temporal information on this type of semantic context effect, indicating left temporal lobe recruitment around 350-400 ms post-stimulus onset. The review by de Zubicaray and Piai (2019) further indicated that modulations of EEG or MEG signal magnitude associated with the distractor contrast occur in a time window between 250-500 ms relative to stimulus onset.

Two picture-word interference studies in individuals with stroke lesions found that the semantic interference effect was not impacted by lesions to the left frontal lobe, but it was impacted by lesions to the left temporal lobe (Piai et al., 2016; Piai & Knight, 2018). Subsequent picture-word interference studies (Pino et al., 2022; Python et al., 2018) suggested that the picture is more complex than the initial studies indicated, but these two studies used distractor presentation preceding picture presentation, a difference in design that reduces the comparability with previous studies using a more typical paradigm without distractor pre-exposure.

Piai et al. (2020) stimulated the left posterior STG or the vertex (i.e., the highest point in the head) as a control site in a picture-word interference task using categorically related and unrelated distractors, in addition to identity distractors. The stimulation covered a window of 400 ms starting with picture-word stimulus onset. The semantic context effect was not affected by posterior STG stimulation (although the identity condition was affected by the stimulation).

A recent picture-word interference study employed NIRS and also observed anterior, mid, and posterior STG/MTG bilaterally, as well as left IFG, associated with the semantic picture-word interference effect (Hitomi et al., 2021). Here, again, the direction of brain activity differences for the related and unrelated conditions were not aligned with the direction of the behavioural effect even within the MTG, with both directions being found in different portions of the gyrus (i.e., both related > unrelated and unrelated > related).

In sum, the semantic context effect in picture-word interference studies is mostly associated with left temporal-lobe structures (albeit with an unclear relationship to the behavioural context effect) and a timing of about 250-500 ms, whereas the evidence regarding the left IFG is mixed.

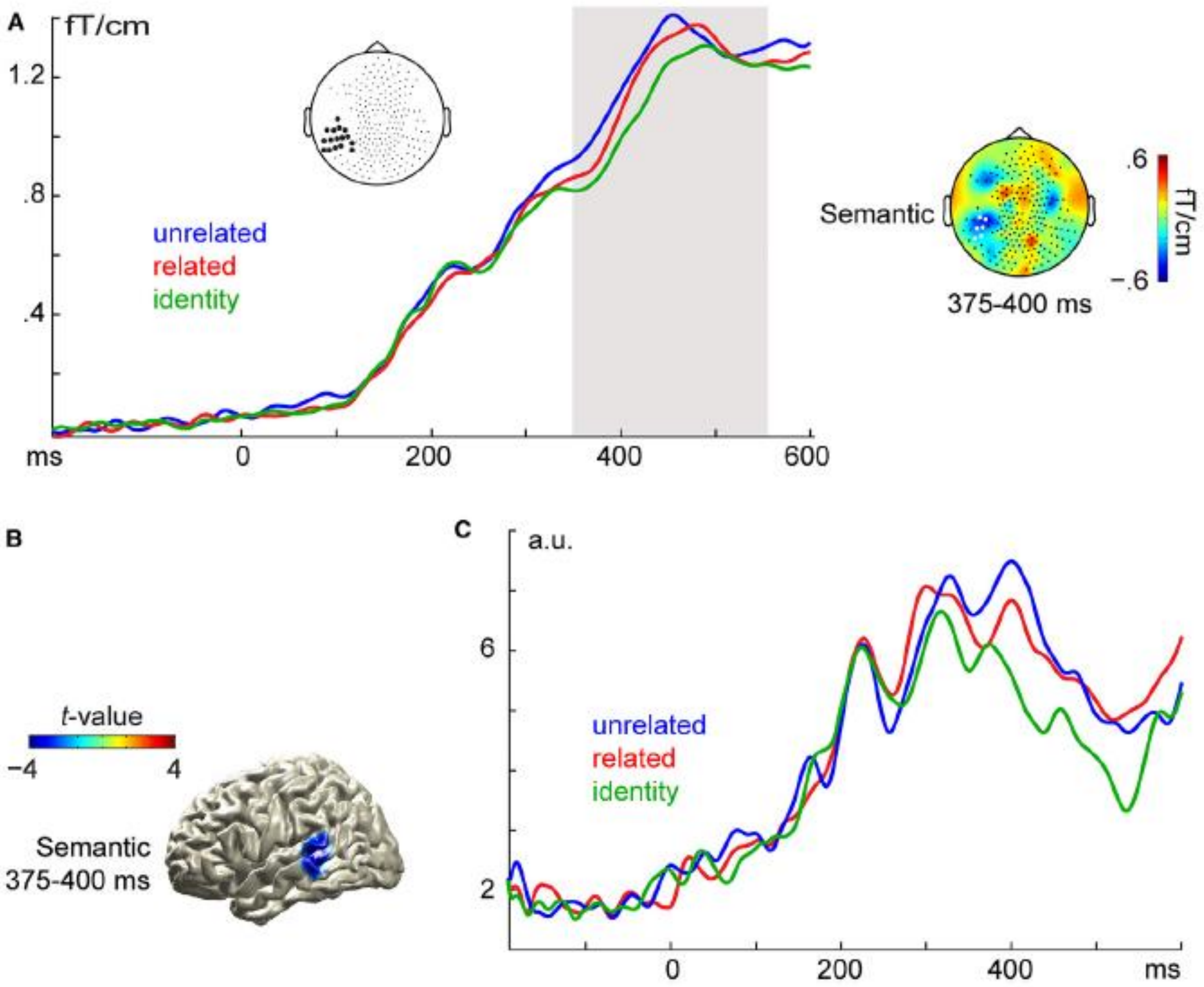

Figure 3. A. Event-related fields (combined planar gradient) for the distractor types, averaged over the left temporal sensors highlighted in the layout in the middle. Note that the "identity" condition is not discussed in the present article. The grey area indicates the window tested for statistical significance. The semantic effect (related vs. unrelated) was characterised by amplitude decrease in left temporal sensors, as shown to the right , between 375–400 ms. The scalp topographies show the difference between conditions averaged in the time window of the corresponding temporal cluster (shown below the topographical map) with the sensors prominent in the cluster highlighted in white. **B.** Estimated sources of the semantic effect in the whole-brain analysis in the time window of the corresponding temporal cluster (shown to the left of the source map). The difference t –value map was thresholded at ±2.16 (13 degrees of freedom, alpha=.05). **C.** Activity from the left temporal cortex (averaged over the estimated sources in B) for the distractor types. Reproduced with permission from the authors from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0088674. Minor changes were made in that the "Stroop-like" effect from the original figure was removed for the reprint.

2.3.2. Blocked-cyclic naming

In the case of the blocked-cyclic naming paradigm, the relevant contrast to study lexical selection is that between homogeneous blocks of categorically related pictures and heterogeneous blocks of unrelated pictures. The semantic interference effect is typically observed starting from the second cycle, whereas semantic facilitation is found in the first cycle (e.g., Belke, 2013). Here, we will refer to both as semantic-block effects and make a distinction in terms of its direction when relevant. Different accounts have been put forward linking this effect to different processes or stages in word production, but the effect has been used extensively to study the overall process of lexical selection (e.g., Belke, 2013; Roelofs, 2018).

As reviewed in de Zubicaray and Piai (2019), one fMRI study identified decreased activity in the left mid and posterior MTG (and hippocampus) for the semantic context effect from the second block onward (de Zubicaray et al., 2014). One MEG study also reported modulations in the left MTG and STG between 150-225 ms associated with the context effect (Maess et al., 2002). The iEEG study by Riès et al. (2017) found modulations of the broadband high gamma signal in left MTG, STG, and ITG, as well as in left frontal regions such as left IFG. Those results showed that the modulations concurrently increased or decreased for homogeneous blocks relative to heterogeneous blocks depending on the brain region. With respect to lesion evidence, studies have also shown both left IFG and left temporal lobe involvement associated with the semantic context effect (Harvey & Schnur, 2015; Riès et al., 2015; Schnur et al., 2009). Finally, using an offline protocol, Krieger-Redwood & Jefferies (2014) applied repetitive TMS to left posterior MTG or left IFG and found that both stimulation sites slowed down naming in the first cycle for the homogeneous blocks.

A more recent study by Anders et al. (2019) using iEEG found converging evidence with the earlier review by de Zubicaray and Piai (2019). Eight out of nine regions showing significant differences between conditions presented reduced activity for the homogeneous blocks relative to the heterogeneous blocks: left anterior fusiform and left anterior ITG, left IFG and middle frontal gyrus, right middle parahippocampal gyrus, right posterior STG, right middle ITG, and right amygdala. In contrast, the medial right superior frontal gyrus showed increased activity in homogeneous relative to heterogeneous blocks. Given the high temporal resolution of the electrophysiological signal, the authors related the time courses of the different regions to picture naming times, as regions showing increased activity above a baseline level only *after* speech has commenced cannot be argued to be involved in lexical selection. The effects found before the mean picture naming latency were in the left anterior ITG between 240 ms and 450 ms post-picture onset, and in the anterior portion of the left fusiform gyrus in a later time window (500 ms to 620 ms).

Python et al. (2018) examined a group of patients with stroke lesions either to the left frontal or left temporal lobes. Contrary to previous studies, neither group showed exacerbated semantic context effects (in either interfering or facilitating direction) relative to the matched control group. Patients with left MTG damage did show increased repetition priming over cycles relative to the control group, which, together with other findings, the authors interpreted as evidence for the involvement of the left MTG in the mapping between semantic concepts and their lexical labels, which is part of the process that we defined as lexical selection.

In sum, and in line with previous conclusions by de Zubicaray and Piai (2019), both left temporal and frontal lobes seem implicated in the semantic-block context effect, with temporal lobe involvement likely around 200-450 ms post picture onset. Although no region can be unambiguously linked to the effect, the prominence of the left temporal lobe in the evidence reviewed here (and its time course) does align with the rest of the findings in the literature with respect to lexical selection and the left temporal lobe.

2.3.3. Continuous naming

In the continuous naming task, the relevant effect is one of increased naming times at each successive picture from a same semantic category, i.e., a cumulative semantic (interference) effect. As previously discussed by de Zubicaray and Piai (2019), one study in individuals with stroke did not find evidence for lesions to the left IFG modulating the cumulative semantic effect (Riès et al., 2015). One fMRI study found that the signal in the left mid portion of the MTG and perirhinal cortex increased linearly with ordinal position, that is, showing a cumulative increase in signal strength (de Zubicaray et al., 2015). The lack of additional studies utilising this paradigm precludes further conclusions with respect to the neural correlates of the cumulative semantic effect.

3. Conclusion

In summary, across different tasks and methodologies, the most prominent areas associated with lexical selection are the (left) temporal lobe (superior, middle, inferior, and fusiform gyri), and, to a lesser extent according to the evidence reviewed, angular and supramarginal gyrus, and inferior frontal gyrus. Even though the evidence points to a prominence for the temporal lobe, it is still somewhat unclear what the relative role is of each gyrus, and perhaps equally important, which portions in the anterior to posterior extent are most prominent (given that the temporal lobe is a large structure). An additional limitation of the approach we took is that the specific processes involved in lexical selection are hard to tease apart from each other, potentially further muddling the picture.

The evidence reviewed in this chapter is also helpful in pointing out the challenge in linking a cognitive operation (lexical selection) to the neural level. Predictions for behavioural tasks based on boxes/nodes from psychological models, be them formal or informal, might result in aligned behavioural results but might not necessarily translate into identifiable physical locations (at the neural level) that perform the exact function of the said box/node in the model (see e.g., Coltheart, 2013 and other articles in that Forum). That is, it is very likely that there is no one-to-one mapping between lexical selection or its sub-processes and certain areas in the brain, with their associated time courses.

Despite these limitations, the converging evidence across tasks and methodologies is reassuring and informative for many practical purposes in clinical settings, for example when planning resective surgeries or towards prognosis following brain damage. The emerging picture brought forth by this concise review will surely consolidate as the field works on improving not only the methods we use, but also the definitions we work with.

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