



The ventrolateral prefrontal cortex facilitates processing of sentential context to locate referents



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ARTICLE INFO

Article history:

Received 23 August 2015

Revised 3 April 2016

Accepted 10 April 2016

Available online 2 May 2016

Keywords:

Sentence comprehension

Eye-tracking

Ventrolateral prefrontal cortex

Inferior frontal gyrus

ABSTRACT

Left ventrolateral prefrontal cortex (VLPFC) has been implicated in both integration and conflict resolution in sentence comprehension. Most evidence in favor of the integration account comes from processing ambiguous or anomalous sentences, which also poses a demand for conflict resolution. In two eye-tracking experiments we studied the role of VLPFC in integration when demands for conflict resolution were minimal. Two closely-matched groups of individuals with chronic post-stroke aphasia were tested: the Anterior group had damage to left VLPFC, whereas the Posterior group had left temporo-parietal damage. In Experiment 1 a semantic cue (e.g., “She will eat the apple”) uniquely marked the target (apple) among three distractors that were incompatible with the verb. In Experiment 2 phonological cues (e.g., “She will see an eagle.”/“She will see a bear.”) uniquely marked the target among three distractors whose onsets were incompatible with the cue (e.g., all consonants when the target started with a vowel). In both experiments, control conditions had a similar format, but contained no semantic or phonological contextual information useful for target integration (e.g., the verb “see”, and the determiner “the”). All individuals in the Anterior group were slower in using both types of contextual information to locate the target than were individuals in the Posterior group. These results suggest a role for VLPFC in integration beyond conflict resolution. We discuss a framework that accommodates both integration and conflict resolution.

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1. Introduction

Left ventrolateral prefrontal cortex (VLPFC) has been implicated in numerous processes, such as semantic processing (e.g., Buckner et al., 1995; Demonet et al., 1992; Fiez, 1997; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Petersen, Fox, Snyder, & Raichle, 1990; Raichle et al., 1994), syntactic processing (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Embick, Marantz, Miyashita, O’Neil, & Sakai, 2000; Grodzinsky, 2000), phonological segmentation and sequencing (Demonet et al., 1992; Newman, Twieg, & Carpenter, 2001; Price et al., 1994; Zatorre, Evans, Meyer, & Gjedde, 1992) and phoneme-to-grapheme conversion processes (e.g., Fiebach, Friederici, Müller, & Von Cramon, 2002), among others. Some have also suggested a domain-general role for this region, in processes such as temporal

sequencing regardless of the specific stimulus type (Gelfand & Bookheimer, 2003).

The present work investigates the role of VLPFC in sentence comprehension, which is most widely proposed to be either semantic integration (e.g., Hagoort, 2005) or conflict resolution (e.g., Novick, Trueswell, & Thompson-Schill, 2005; Nozari & Thompson-Schill, 2015). Semantic integration refers to a process whereby the representation of the incoming word is bound to the representation constructed from previous words in the sentence (e.g., Hagoort, 2005). Conflict resolution refers to an executive operation through which processing is biased towards the relevant and away from the irrelevant information (e.g., Nozari & Thompson-Schill, 2013). These two proposals are, by no means, mutually exclusive. If at any point during the integration process there are competing representations (e.g., when one meaning of a homophone must be selected (Bedny, McGill, & Thompson-Schill, 2008; Hagoort, 2005; Lau, Phillips, & Poeppel, 2008)), conflict resolution is required. However, integration would still be needed for sentence comprehension even in the absence of strong

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competition. This study examines if VLPFC has a role in semantic integration when competition is controlled for.

1.1. VLPFC and conflict resolution

As discussed above, the conflict resolution account proposes a domain-general role for the VLPFC in resolving competition between multiple incompatible representations of a stimulus by biasing processing toward task- or context-appropriate information (Thothathiri, Kim, Trueswell, & Thompson-Schill, 2012). This may happen as part of semantic integration during sentence comprehension, for example, processing sentences containing ambiguous words elicits VLPFC activation (e.g., Rodd, Davis, & Johnsrude, 2005; Rodd, Johnsrude, & Davis, 2012; Rodd, Longe, Randall, & Tyler, 2010; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007), which can activate conflicting meanings. Similarly, VLPFC is activated when encountering garden-path sentences (January, Trueswell, & Thompson-Schill, 2009; Novick, Kan, Trueswell, & Thompson-Schill, 2009; Novick et al., 2005), which can activate conflicting syntactic trees. The idea is that VLPFC starts to bias processing at the moment the parser encounters an ambiguity and continues to update the bias as more information accumulates. If the parser is biased towards the incorrect interpretation, the later the disambiguating information comes in, the more work needed to shift the competition in favor of the alternative meaning, and the greater the VLPFC activation. Thus, VLPFC activation must correlate with the distance between the point of ambiguity and the point of disambiguation. In agreement with this prediction, VLPFC activation is greater when disambiguating information comes later rather than earlier in a sentence (Fiebach, Schlesewsky, Lohmann, Von Cramon, & Friederici, 2005). Also, when the relative timing of an ambiguous word and the disambiguating information is manipulated, VLPFC activation is induced both by the ambiguous word and by the disambiguating information, two points in the sentence where biasing competition was necessary (Rodd et al., 2012).

Nozari and Thompson-Schill (2015) reviewed a large body of literature linking VLPFC to comprehension of sentences with syntactic complexity, ambiguity, anomaly, and reasoned that all such cases require resolution of conflict between competing representations (see also Kaan & Swaab, 2002). However, all of these cases fit with the semantic integration account as well: the goal of selecting the relevant information is to construct a coherent representation that could convey an unambiguous message. Thus, the two proposals cannot be distinguished based on experiments in which sentence comprehension requires conflict resolution. Validation of the conflict resolution proposal requires demonstrating that VLPFC is involved in cases where integration into sentential context is not relevant. There are numerous examples of this in the literature, some of which we review below.

An early demonstration of VLPFC activation outside of sentence comprehension was provided through three experiments by Thompson-Schill, D'Esposito, Aguirre, and Farah (1997). VLPFC was found to be more activated when (1) matching a picture (e.g., car) to an attribute (e.g., "expensive") compared to its name ("car"), (2) when similarity of items was to be judged based on a specific feature (e.g., feature "white" for judging the similarity between tooth, bone and tongue), ignoring other features, compared to when global similarity was the basis of judgment, and (3) when verbs were to be generated in answer to items that were associated strongly with a single verb (e.g., scissors → cut) than with many possible verbs (e.g., cat → eat, meow, play, etc.). Numerous other studies have also shown VLPFC activation outside the domain of sentence comprehension. Among these are living/nonliving classification (Demb et al., 1995; Gabrieli et al., 1996; Kapur et al., 1994), feature-based similarity judgment (e.g.,

Whitney, Kirk, O'Sullivan, Ralph, & Jefferies, 2011), category-based verbal fluency (Basho, Palmer, Rubio, Wulfeck, & Müller, 2007; Birn et al., 2010), and Stroop and working memory tasks (Milham, Banich, & Barad, 2003; Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003). Moreover, while certain regions of LPFC are sensitive to the stimulus type, the pattern of activity for spatial and verbal information is indistinguishable along LPFC's rostro-caudal axis (e.g., Bahlmann, Blumenfeld, & D'Esposito, 2015), pointing to some level of domain-general activity of this area in carrying out executive control (e.g., Fedorenko & Thompson-Schill, 2014).

In summary, the activation of VLPFC during a variety of tasks and across various modalities builds a strong case for its involvement in a domain-general executive function, one that we have argued is biasing competition. This naturally extends to processing sentences in which conflict resolution is frequently required, hence explaining why this region would be activated when individuals attempt to comprehend sentences with semantic or syntactic anomaly or ambiguity. The critical question is whether VLPFC has any role beyond this in sentence comprehension.

2. VLPFC and integration

The bulk of evidence for the role of VLPFC in integration comes from studies showing the region's increased activity when a sentence contains an anomaly (Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kiehl, Laurens, & Liddle, 2002; Kuperberg, 2007; Kuperberg et al., 2000; Kuperberg, Caplan, Sitnikova, Eddy, & Holcomb, 2006; Kuperberg, Sitnikova, & Lakshmanan, 2008; Kuperberg et al., 2003; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003; Newman et al., 2001; Ni et al., 2000). The type of anomaly does not seem to be critical for VLPFC activation. While not all similar in their EEG footprints, syntactic violations (e.g., "at breakfast the boys would eats..."), semantic violations in the absence of syntactic violations (e.g., "at breakfast the eggs would eat..."), violation of world knowledge (e.g., "The Dutch trains are white...") or unexpected events (e.g., "...at breakfast the boys would plant...") all have been shown to activate VLPFC (e.g., Kuperberg et al., 2008).

Anomalies need not be confined to the linguistic system to recruit VLPFC. Willem, Özyürek, and Hagoort (2007) showed that VLPFC responded to mismatch not only within the linguistic domain (e.g., the Dutch version of "He should not forget the items he hit on the shopping list."), but also to a mismatch between the linguistic and gestural information (e.g., watching the hitting action while listening to a linguistically sound sentence such as "He should not forget the items he wrote on the shopping list."). In the same vein, Tesink et al. (2009) showed bilateral activation of VLPFC when the semantic content of the sentence did not match the speaker's characteristics such as age, sex and social background implied by the speaker's voice. For example, although "Every evening I drink a glass of wine before going to bed" is semantically and syntactically sound, it is unexpected from a child.

As discussed earlier, the increased activation of VLPFC in anomalous vs. correct sentences is also compatible with a conflict resolution account, because when the expected and the actual outcomes clash, two representations are competing for selection. A few studies claim that VLPFC activation is not limited to cases with conflicting information. For example, VLPFC activation was also observed when speaker's characteristics matched the content of the sentence (Tesink et al., 2009, Fig. 1). Note, however, that this claim is based on a comparison between processing non-anomalous sentences and rest. It is therefore hard to argue that VLPFC activation during processing of such sentences spoke specifically to integration as opposed to any number of processes involved in sentence comprehension.

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