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Right semantic modulation of early MEG components during ambiguity resolution

Yuval Harpaz [a,c], Michal Lavidor [b,c], Abraham Goldstein [b,c,*]

[a] Department of Psychology, Tel-Aviv University, Tel-Aviv, Israel
[b] Department of Psychology, Bar-Ilan University, Ramat Gan, Israel
[c] Gonda Brain Research Center, Bar-Ilan University, Ramat Gan, Israel

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ABSTRACT

The time-line of lexical ambiguity resolution in bilateral neuronal networks was investigated using magnetoencephalography (MEG) in a semantic decision task. Dominant and subordinate associations of ambiguous words are considered to be processed in the left and right hemispheres, respectively. In the experiment, ambiguous words were followed by dominant or subordinate associations (manipulated between blocks) or by unrelated target words, and participants (N = 25) decided whether the words in each pair were related or not. Subordinate meaning blocks elicited greater changes in the magnetic fields relative to dominant ones over the right, but not the left hemisphere (LH) at 150–235 ms from target onset, a time window corresponding to the M/N170 M/EEG component. Beamforming analysis localized the differential right hemisphere (RH) activity at the perisylvian area, including the homologue regions of Broca's and Wernicke's. At a later stage (235–390 ms) there was no significant difference between the two meaning conditions. We suggest that the RH language regions assist the LH in integrating subordinate disambiguating clues to preceding context during the M170 time window.

Introduction

General introduction

It is widely believed that for over 90% of the population both language and handedness are lateralized to the left hemisphere (LH; Tzourio-Mazoyer et al., 2010). A major evidence for the laterality of language is the fact that damage to LH language regions often leads to aphasia while RH damage causes aphasia only in rare cases (Faglia et al., 1990). Therefore, the RH is generally considered to play a minor role in simple language processing. However, the RH is hypothesized to participate in language processing along with the dominant left hemisphere in situations with complex content such as a joke or an indirect request (Gardner and Brownell, 1986; Gardner et al., 1975; Zaidel, 2001). Gazzaniga (1983) suggested that a possible role of the RH is to assist the left hemisphere (LH) by validating one out of few possible interpretations. The general aim of this work is to explore the regions and time-course of activity of RH language function. To that purpose, we chose to focus on a task involving ambiguous words (*bank*) with dominant (*money*) and subordinate associations (*river*). This allows manipulating the complexity levels using relatively simple stimuli. We expected to measure increased activity over the RH when dealing with subordinate, compared to the dominant associations, and planned to estimate the timing and location of the increased activity.

Ambiguous words processing

Some ambiguous words are biased to one dominant meaning (Burgess and Simpson, 1988) which is their frequent (Rayner and Frazier, 1989) or salient (Giora, 2007) meaning. The other meaning is called subordinate. When one reads a sentence containing a biased ambiguous word such as "I went to the *bank* and it was closed" the word bank is interpreted without difficulty because its dominant meaning (financial institution), is relevant to the sentential context. The sentence "I went to the *bank* and the boat wasn't there" introduces a difficulty because the dominant meaning is irrelevant. When one reads the word *boat* (disambiguating clue) the reader realizes that *bank* more probably stands for a river bank which is its subordinate, or less frequent, meaning. It has been shown in gaze studies (Rayner and Frazier, 1989) that special effort in disambiguation (of biased words) is required for subordinate meanings while dominant meanings are processed similarly to unambiguous words.

Theoretical background

Jung-Beeman's model (2005) for fine and coarse semantic coding advocates that biased ambiguous words activate their subordinate, as well as their dominant, meanings in the right homologue of

Abbreviations: IFG, inferior frontal gyrus; LH, left hemisphere; RH, right hemisphere; RMS, root mean square.

* Corresponding author at: Department of Psychology, Bar-Ilan University, Ramat Gan 52900 Israel. Fax: +972 35349353.
E-mail address: goldsa@mail.biu.ac.il (A. Goldstein).

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Wernicke's area. As soon as a subsequent subordinate association word appears, the right anterior temporal lobe attempts to integrate its meaning with the pre-activated meanings of the ambiguous word. This process is followed by the selection of the relevant concept in the right inferior frontal gyrus (IFG; see also at Thompson-Schill et al., 1997). Federmeier and Kutas (1999) also suggested that the RH contributes to ambiguity resolution by integrating subordinate meanings to context (see also the PARLO framework, Federmeier, 2007), whereas the LH specializes in prediction. Thus, according to both models subordinate meanings should activate RH more than dominant meanings.

Many studies on ambiguity processing have used tasks which did not require explicit ambiguity resolution (e.g., Bilenko et al., 2009; Burgess and Simpson, 1988; Copland et al., 2007; Grindrod and Baum, 2003; Klepousniotou, 2002; Peleg and Eviatar, 2008). However, since our purpose was to explore the neuronal correlates of left and right semantic processing the current study employed explicit semantic processing of word pairs consisting of biased ambiguous words coupled with disambiguation words or unrelated ones. The task was to indicate by button press whether the second word was related to the first or not. Therefore, in order to respond correctly subjects had to resolve the ambiguity. Previous language laterality studies with explicit semantic processing of ambiguous words have used visual hemifield presentation (Faust and Lavidor, 2003; Harpaz and Lavidor, 2012), transcranial magnetic stimulation location (Harpaz et al., 2009), fMRI activation (Zempleni et al., 2007) and lesion site (Gardner and Brownell, 1986; Zaidel et al., 2002). These studies generally concluded that the RH participates in ambiguity resolution. However, the methods used in these studies do not allow fine spatio-temporal resolution and therefore it is impossible to deduce from these studies when each brain region was active. The time course of brain activity during word reading has been examined using EEG/MEG measures that have adequate temporal resolution. It is commonly viewed that the orthographic decoding is manifested early on in the N170 component (Bentin et al., 1999; Cohen et al., 2000). There is also agreement that the N400 (M350) component reflects semantic processing (see review: Pammer, 2009). However, some studies (Dell'Acqua et al., 2007; Pulvermüller et al., 2001; Sereno et al., 1998) have found evidence for semantic processing less than 200 ms after word onset. An EEG study of lexical ambiguity that used the N400 amplitude as a metric for semantic processing found evidence for hemispheric asymmetry in ambiguous word processing at this stage (Atchley and Kwasny, 2003). Brain responses to related and unrelated ambiguous words differed when presented to the LH, but not when presented to the RH. This suggested that the very broad representation of an ambiguous word in the RH does not generate semantic expectations (thus no N400 difference). In contrast, in the LH unrelated words elicited higher N400 amplitude than the dominant related words. A differential response was found in the LH also for subordinate meanings, although it was significantly delayed. The insensitivity of the N400 component to subordinate meanings in left visual field trials may imply that the RH did not contribute to semantic processing. This stresses the importance of finding the conditions in which the RH *does* contribute.

Paradigm and predictions

The current work aimed to define the time-course of RH activity during lexical ambiguity resolution. In order to maximize the involvement of the RH in the task, we measured the brain activity elicited by subordinate associations of biased ambiguous words and compared it with the responses to dominant associations. The stimulus onset asynchrony was set over 750 ms to allow the meanings of the ambiguous words to be activated in the two hemispheres before the display of the disambiguation clue (Burgess and Simpson, 1988; Frost and Bentin, 1992). The meaning (dominant vs. subordinate) was manipulated between blocks, since it had been found that the blocked design facilitates hemispheric expertise for ambiguity processing, possibly through conditioning the brain to use the expert hemisphere according to block meaning (Harpaz and Lavidor, 2012). We employed a semantic decision task to ensure that the correct meaning of the ambiguous words was processed. Trials with words unrelated to the ambiguous word served mainly as filler items and were necessary for setting the rate of positive answers at 50%, thus avoiding response bias. The contrast of interest was the difference in brain activity elicited by subordinate relative to dominant meaning words. We predicted that the comparison between subordinate and dominant related associations would reveal greater activity in RH language regions. Furthermore, we examined whether the conditions would help reveal RH contribution at early stages of processing.

Methods

Participants

Twenty five students (4 male, mean age 29.6) participated after giving informed consent. All were right-handed (scoring at least 90 on the Edinburgh Handedness inventory; Oldfield, 1971) native Hebrew speakers. Their sight was normal or corrected to normal.

Design

A factorial 2 × 2 design was applied, with meaning (dominant, subordinate) and relatedness (related, unrelated) as within subject factors. The unrelated trials were used in this study only as filler trials to allow the semantic task and were not analyzed.

Visual stimuli

A list of 90 ambiguous Hebrew words (with no vowel markings) and their dominant and subordinate associations taken from previous studies (Faust and Kahana, 2002; Harpaz et al., 2009; Peleg and Eviatar, 2008; see example stimuli in Fig. 1) was used for the related trials. A separate list of 90 ambiguous words, paired with unrelated words was used for the unrelated trials. Dominant and subordinate association words, as well as unrelated association words, were matched in terms of length (number of letters) and frequency (Frost and Plaut, 2005). The mean length was 4.24 letters for all the conditions with no significant difference between them ($p > 0.3$). The average frequency of the target words was 41 and 39 per million for the dominant and subordinate blocks, respectively, and was not statistically different ($p > 0.3$).

The words were presented in the center of the screen in Courier New, size 18 such that the average stimulus (4.17 letters) subtended 3.0° of visual angle. Letters were black on a gray background, projected through a mirror on a screen located 55 cm from the participant's head.

Procedure

Five coils were attached to the participant's scalp for recording the head position relative to the sensor. The head-shape was digitized

Word-pair type	Ambiguous word	Target word
Dominant related	הנחה	הוזלה
	discount	price reduction
Subordinate related	הנחה	השערה
	assumption	hypothesis
Unrelated	טון	נמנע
	ton / pitch	avoids

Fig. 1. Example word-pairs.