Neuropsychology

Phonological Ambiguity Modulates Resolution of Semantic Ambiguity During Reading: An fMRI Study of Hebrew

Tali Bitan, Asaf Kaftory, Adi Meiri-Leib, Zohar Eviatar, and Orna Peleg

Online First Publication, August 31, 2017. http://dx.doi.org/10.1037/neu0000357

CITATION

Bitan, T., Kaftory, A., Meiri-Leib, A., Eviatar, Z., & Peleg, O. (2017, August 31). Phonological Ambiguity Modulates Resolution of Semantic Ambiguity During Reading: An fMRI Study of Hebrew. *Neuropsychology*. Advance online publication. http://dx.doi.org/10.1037/neu0000357

Neuropsychology

0894-4105/17/$12.00 http://dx.doi.org/10.1037/neu0000357

Phonological Ambiguity Modulates Resolution of Semantic Ambiguity During Reading: An fMRI Study of Hebrew

Tali Bitan, Asaf Kaftory, Adi Meiri-Leib,
and Zohar Eviatar
University of Haifa

Orna Peleg
Tel-Aviv University

Objectives: The current fMRI study examined the role of phonology in the extraction of meaning from print in each hemisphere by comparing homophonic and heterophonic homographs (ambiguous words in which both meanings have the same or different sounds respectively, e.g., *bank* or *tear*). The analysis distinguished between the first phase, in which participants read ambiguous words without context, and the second phase in which the context resolves the ambiguity. ***Method:*** Native Hebrew readers were scanned during semantic relatedness judgments on pairs of words in which the first word was either a homophone or a heterophone and the second word was related to its dominant or subordinate meaning. ***Results:*** In Phase 1 there was greater activation for heterophones in left inferior frontal gyrus (IFG), pars opercularis, and more activation for homophones in bilateral IFG pars orbitalis, suggesting that resolution of the conflict at the phonological level has abolished the semantic ambiguity for heterophones. Reduced activation for all ambiguous words in temporo-parietal regions suggests that although ambiguity enhances controlled lexical selection processes in frontal regions it reduces reliance on bottom-up mapping processes. After presentation of the context, a larger difference between the dominant and subordinate meaning was found for heterophones in all reading-related regions, suggesting a greater engagement for heterophones with the dominant meaning. ***Conclusions:*** Altogether these results are consistent with the prominent role of phonological processing in visual word recognition. Finally, despite differences in hemispheric asymmetry between homophones and heterophones, ambiguity resolution, even toward the subordinate meaning, is largely left lateralized.

General Scientific Summary
The study examined access to meaning from print using ambiguous words. Resolution of words with different sounds (*tear*) involves mainly brain regions specialized for processing word sounds, whereas the conflict in ambiguous words with 1 sound (*bank*) is processed at the level of meaning. This shows the prominent role of sound processing even when reading familiar words. This process is more left lateralized than processing of word meaning.

Keywords: ambiguous words, reading, fMRI, hemispheric lateralization, phonology

Supplemental materials: http://dx.doi.org/10.1037/neu0000357.supp

The main goal of the current study is to examine the interactions between orthography, phonology and semantic processing in the two hemispheres. In particular, we examined the role phonology plays in the extraction of meaning from print by comparing the disambiguation process of two types of ambiguous words: homophones (in which both meanings have the same sounds; e.g., *bank*) and heterophones (in which the two meanings have different sounds; e.g., *tear*). The second goal of this fMRI study was to dissociate between lexical and contextual effects in ambiguity resolution.

The Role of Phonology in Extraction of Meaning From Print

In principle, there are two possible ways to extract meaning from print: orthographically—from orthography directly to meaning, or phonologically—from orthography to phonology to meaning. Different theories of visual word recognition have placed different emphases on these two pathways. On the one hand, dual route (e.g., Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001) and other reading models (Rayner, Pollmann, Ashby, & Clifton,

---

Tali Bitan, Asaf Kaftory, Adi Meiri-Leib, and Zohar Eviatar, Psychology Department, Institute of Information Processing and Decision Making, University of Haifa; Orna Peleg, The Cognitive Studies of Language Program, School of Cultural Studies, Tel-Aviv University.

This work was funded by the Israel Science Foundation (ISF) grant 1090/08 to Orna Peleg and Zohar Eviatar.

Correspondence concerning this article should be addressed to Tali Bitan, Psychology Department, Institute of Information Processing and Decision Making, University of Haifa, 199 Aba-Hushi Avenue, Mount Carmel, Haifa 3498838, Israel. E-mail: tbitan@research.haifa.ac.il

2012) assume that skilled word recognition is driven primarily by orthography via the direct lexical route. On the other hand, the strong phonological hypothesis (e.g., Frost, 1998) suggests that phonological recoding is an early, mandatory (automatic) phase of print processing. Between these two positions, connectionist triangle models (Harm & Seidenberg, 2004; Seidenberg & McClelland, 1989) suggest that semantic patterns reflect the joint effects of both orthographic and phonological sources of information.

Consistent with both dual route (e.g., Coltheart et al., 2001) and connectionist triangle models (e.g., Harm & Seidenberg, 2004), fMRI studies that investigated the brain areas associated with reading alphabetic languages have located a reading network in the left hemisphere (LH) with two major pathways: a lexicosemantic ventral pathway and a phonological dorsal pathway supporting the conversion of print-to-sound (Price, 2012). The ventral lexicosemantic route integrates information from the left fusiform, middle temporal gyrus, angular gyrus, and the inferior frontal gyrus pars triangularis and pars orbitalis. The dorsal orthographic-phonological pathway, on the other hand, involves supramarginal gyrus (SMG), inferior parietal lobule (IPL), and the inferior frontal gyrus pars opercularis (Carreiras, Armstrong, Perea, & Frost, 2014; Dehaene, 2009; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Taylor, Rastle, & Davis, 2013; Vigneau et al., 2006). Nevertheless, a major difference between dual route models and connectionist "triangle" models is the degree to which these two pathways interact during reading. In particular, although dual route models assume that familiar words are recognized orthographically via the direct lexical route, connectionist models assume that visual word recognition always involves a dynamic interplay between orthographic, phonological, and semantic processes. Furthermore, although skilled reading is typically associated with a left lateralized network, it is now well established from both behavioral studies (e.g., Faust & Chiarello, 1998; Marsolek, Kosslyn, & Squire, 1992; Marsolek, Schacter, & Nicholas, 1996; Ripamonti, Traficante, Crippa, & Luzzattii, 2014; Titone, 1998; Zaidel, 1998; Zaidel & Peters, 1981) and neuroimaging studies (e.g., Federmeier & Kutas, 1999; Jung-Beeman, 2005; Vigneau et al., 2011) that both hemispheres can process the meanings of written words, albeit in qualitatively different ways. The present fMRI study therefore aimed to investigate how orthographic, phonological, and semantic codes interact in the two cerebral hemispheres during the processing of familiar written words.

Hemispheric Differences in Orthographic, Phonological and Semantic Processing

Behavioral studies using the divided visual field (DVF) technique[1] reported hemispheric differences in orthographic (e.g., Lavidor & Ellis, 2003), phonological (e.g., Halderman & Chiarello, 2005), and semantic processing (e.g., Burgess & Simpson, 1988). However, the extent to which these three sources of information interact, within each hemisphere, is relatively unexplored, because hemispheric differences in sublexical orthographic and phonological processing were typically studied separately from semantic asymmetries. In particular studies that focused on sublexical orthographic/phonological asymmetries show that visual word recognition in the LH is influenced by both orthographic and phonological sources of information, whereas word recognition processes in the right hemisphere (RH) are mainly influenced by orthography (e.g., 2005; Lavidor & Ellis, 2003; Peleg, Markus, & Eviatar, 2012; Peleg & Eviatar, 2009; Smolka & Eviatar, 2006; Zaidel & Peters, 1981). These conclusions are consistent with findings from neuroimaging studies in language processing, more generally, showing LH specialization for (sublexical) phonological processes (Hickok & Poeppel, 2007; Vigneau et al., 2011). However, evidence for mandatory (sublexical) phonological activations in the LH, do not necessarily entail that access to meaning in this hemisphere is predominantly phonologically mediated. In other words, it is possible that the focus on phonological tasks (e.g., rhyme judgments) or nonwords (e.g., pseudohomophones) has highlighted the role of left lateralized phonology in reading.

Similarly, studies on hemispheric differences in meaning processing did not take into account lower-level orthographic/phonological asymmetries. These studies have led to the conclusion that the two hemispheres differ in their ability to carry out meaning selection. According to this received view, when readers encounter an ambiguous word (e.g., *bank*), the LH quickly selects the dominant, more salient meaning (when context is not provided), or the contextually appropriate meaning (when context is provided). In contrast, the RH maintains activation of multiple meanings including those that are less salient or inconsistent with the context (e.g., Burgess & Simpson, 1988; Faust & Chiarello, 1998; Faust & Gernsbacher, 1996; Jung-Beeman, 2005). However, because an orthographic representation of an English word (as well as other Latin orthographies) is usually associated with one phonological representation, most studies on semantic ambiguity resolution used homophonic homographs (e.g., *bank*)—multiple meanings associated not only with a single orthographic representation but also with a single phonological representation. As a result, the relative contribution of orthographic and phonological sources of information to meaning activation and selection processes in the two hemispheres is impossible to determine. As detailed below, the present study used the unique characteristics of Hebrew to directly investigate how orthographic, phonological, and semantic representations interact in the two cerebral hemispheres.

The Disambiguation of Homophonic Versus Heterophonic Homographs

In Hebrew, letters represent mostly consonants and vowels can optionally be superimposed on consonants as diacritical marks. Because the vowel marks are usually omitted, Hebrew readers frequently encounter not only homophonic homographs (e.g., *bank*), but also heterophonic homographs (e.g., *tear*). Both types of homographs have one orthographic representation associated with two different meanings; they are different however in terms of the relationship between orthography and

---

[1] This technique takes advantage of the fact that stimuli presented in the left side of the visual field are initially processed by the right hemisphere and vice versa. Although information presented in this manner can later be transmitted to both hemispheres, the interpretation of DVF paradigms rests on the assumption that responses to stimuli presented briefly to one visual field, reflect mainly the processing of that stimulus by the contralateral hemisphere, so that responses to targets in the right visual field reflect left hemisphere processes, and responses to targets in the left visual field reflect processes in the right hemisphere (for theoretical and electrophysiological support for this assumption, see Banich, 2003; Berardi & Fiorentini, 1997; Coulson, Federmeier, Van Petten, & Kutas, 2005).

phonology, and between phonology and semantics. In the case of homophonic homographs (*bank*), the orthographic representation is associated with a single phonological code that is associated with both meanings. In the case of heterophonic homographs (*tear*), the orthographic representation is associated with two different pronunciations (/tIər/ /tɛər/), each associated with a different meaning. If meanings are extracted directly from print, as assumed by the dual route model (e.g., Coltheart et al., 2001), then homophonic and heterophonic homographs should be processed similarly. Alternatively, if reading is phonologically mediated, as assumed by the strong phonological hypothesis (e.g., Frost, 1998) or by connectionist triangle models (e.g., Harm & Seidenberg, 1999; Seidenberg & McClelland, 1989), then these two types of homographs are expected to show different patterns of activation of their competing meanings, because accessing the multiple meanings of heterophones requires the activation of multiple phonological forms, whereas accessing the multiple meanings of homophones does not. Moreover, if direct orthographic-phonological connections are available only to the LH, as demonstrated by studies using nonwords (e.g., Halderman & Chiarello, 2005), then these different patterns of activation should be observed in the LH, but not in the RH.

Peleg and Eviatar (2008, 2009) used the behavioral DVF technique to examine hemispheric asymmetries in accessing and maintaining distinct meanings of these two types of Hebrew homographs. Consistent with previous studies (e.g., Halderman & Chiarello, 2005), phonological effects (differences between homophonic and heterophonic homographs) were more pronounced in the LH than in the RH. In particular, when homographs were presented without a biasing context, in the RH, subordinate meanings were activated together with dominant meanings irrespective of homograph type. In contrast, in the LH, different patterns were observed for the two types of homographs. In the case of homophonic homographs, both dominant and subordinate meanings were activated immediately, but shortly afterward only the dominant meaning remained active. Importantly, in the case of heterophonic homographs, dominant meanings were activated exclusively. The finding that only the LH was sensitive to the difference between homophones and heterophones suggests, not only that direct orthographic-phonological links are available only to the LH, but that these early orthographic-phonological processes may precede orthographic-semantic processes. As a result, in the case of homophonic homographs (*bank*), the shared phonological code automatically activates both meanings. Alternatively, in the case of heterophonic homographs (*tear*), presemantic phonological disambiguation inhibits activation of the subordinate meaning.

To further investigate the interaction between phonological and semantic processes in silent reading, the main goal of the current study was to directly compare the pattern of brain activity associated with the processing of three types of words: homophonic homographs, heterophonic homographs, and unambiguous words, which differ in their relationship between orthography, phonology and meaning. To the best of our knowledge, this is the first fMRI study to investigate the neural activity associated with the processing of heterophonic homographs (which are rare in English, but very common in Hebrew). Nevertheless, a number of studies have used homophonic homographs to investigate how the brain copes with semantic ambiguity (e.g., Mason & Just, 2007; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007).

Brain Activity Patterns in Processing Semantic Ambiguity

Ample evidence from behavioral and neuroimaging research indicates that the processing of lexically ambiguous words is influenced by both lexical (e.g., degree of meaning dominance) and contextual sources of information (Duffy, Morris, & Rayner, 1988; Giora, 2003; Peleg, Giora, & Fein, 2001, 2004). When reading sentences with ambiguous words was compared to sentences with less or no ambiguous words, greater activation was found in the posterior aspect of left inferior frontal gyrus (LIFG; Mason & Just, 2007; Zempleni et al., 2007). Part of this region (LIFG pars triangularis) was also more active for the comparison of the subordinate and the dominant meaning (Zempleni et al., 2007). These studies attributed activation in posterior LIFG to greater processing demands in retrieval and selection of the meanings during integration with sentential context information. However, activation in this region, is also found in listening to ambiguous sentences (Rodd, Davis, & Johnsrude, 2005; Vitello, Warren, Devlin, & Rodd, 2014), reading syntactically ambiguous sentences (Snijders et al., 2009) and processing of ambiguous single words (Bilenko, Grindrod, Myers, & Blumstein, 2009; Ihara et al., 2015; Newman & Joanisse, 2011). This recruitment of left posterior inferior frontal gyrus (IFG) in the resolution of many types of ambiguities may indicate its involvement in a more general cognitive control process within the language network (Bedny, Hulbert, & Thompson-Schill, 2007; Bedny, McGill, & Thompson-Schill, 2008; Gold, Balota, Kirchhoff, & Buckner, 2004; January, Trueswell, & Thompson-Schill, 2009; Novick, Trueswell, & Thompson-Schill, 2005; Taylor et al., 2013).

Although theoretical approaches (Jung-Beeman, 2005) and behavioral studies (e.g., Faust & Chiarello, 1998) suggest a unique role for the RH in activating and maintaining alternative meanings of ambiguous words, the pattern of findings from different neuroimaging studies do not provide clear evidence for such hemispheric lateralization. Several neuroimaging studies report RH or bilateral activation in IFG in reading ambiguous compared to unambiguous sentences (Zempleni et al., 2007) or single words (Bilenko et al., 2009), and in listening to ambiguous sentences (Rodd et al., 2005). The right IFG was also more active for sentences biased toward the subordinate meaning compared to the dominant meaning (Mason & Just, 2007). RH activation was also reported in the temporo-parietal junction (TPJ) primarily for visually presented ambiguous words. Specifically this was found in the right IPL (Chan et al., 2004; Ketteler, Kastrau, Vohn, & Huber, 2008; Ketteler et al., 2014; Newman & Joanisse, 2011) and the right SMG (Klepousniotou, Gracco, & Pike, 2014), which are homologous to regions typically involved in mapping of orthography to phonology in reading (Bitan et al., 2007; Hartwigsen et al., 2010; Price, 2012; Taylor et al., 2013). However, it is still unclear whether the RH plays a special role in processing ambiguous more than unambiguous words because some of these studies compared ambiguous words to a nonlinguistic baseline such as symbol strings, rather than to unambiguous words (Klepousniotou et al., 2014). It is also unclear if the RH is more active than the LH because previous studies did not quantify the comparison between hemispheres. However, one transcranial DC stimulation study showed that excitatory stimulation over the right temporal cortex facilitated processing of the subordinate meaning of ambiguous words while stimulation of the left temporal cortex did not (Peretz & Lavidor, 2013). Altogether the RH may be involved specifically in access and maintenance of the subordinate meaning or be recruited more generally due to increased task demands.

All of the above studies focused on homophonic homographs (e.g., *bank*), whose ambiguity can only be resolved at the semantic level. Heterophonic homographs (e.g., *tear*), on the other hand, can also be resolved at the phonological level, which is expected to be more left lateralized (Hickok & Poeppel, 2007; Vigneau et al., 2011). Thus, if heterophonic homographs are disambiguated phonologically rather than semantically (Peleg et al., 2012; Peleg & Eviatar, 2009, 2012), we expect less involvement of the RH in the resolution of heterophones compared to homophones. In addition to the comparison between homophones and heterophones (phonological disparity), the second goal of this study was to dissociate between lexical and contextual effects in ambiguity resolution. Most fMRI studies did not distinguish between two distinct phases of processing semantic ambiguity: the conflict between competing lexical representations encountered when reading an ambiguous word without a context and the resolution of this conflict when a biasing context is provided. The first phase may involve a selection of the dominant meaning (meaning salience; e.g., Burgess & Simpson, 1988; Duffy et al., 1988), whereas in the second phase the ambiguous word is integrated with the context (e.g., Duffy et al., 1988; Faust & Chiarello, 1998). Few studies that attempted to make the distinction between these phases suggest the LIFG is involved both at the early stage, retrieval of multiple meanings of the ambiguous word, as well as at the later stage of selection between these meanings (Acheson & Hagoort, 2013; Ihara, Hayakawa, Wei, Munetsuna, & Fujimaki, 2007; Rodd, Johnsrude, & Davis, 2012). However, these studies examined spoken sentences (Rodd et al., 2012) or presented the context prior to the ambiguous word (Ihara et al., 2007).

The Present Study

Thus, although the main goal of the current study was to compare the pattern of brain activity associated with the processing of homophonic and heterophonic homographs, the second goal was to separate between the two phases in reading ambiguous words. This was done by using fMRI that enables to examine multiple brain regions simultaneously, and by using a region of interest (ROI) analysis that enables to directly compare between the two hemispheres. We have also used an experimental design that enables independent modeling of events within trials (Ollinger, Shulman, & Corbetta, 2001).

In this study, adult Hebrew readers were scanned while performing a semantic relatedness judgment task on pairs of visually presented words. The first word in the pair (Phase 1) was either a homophone, a heterophone or an unambiguous word. The second word in each pair (Phase#2: "the context") was always unambiguous and could be related to either the dominant or subordinate meanings (in case of homographs, or related to the only meaning in case of unambiguous words) or unrelated to the first word. ROI analyses were conducted in regions previously shown to be involved in reading ambiguous words, namely bilateral IFG (e.g., Bilenko et al., 2009; Mason & Just, 2007; Rodd et al., 2005; Zempleni et al., 2007) divided into its three constituent sub regions: Opercularis, triangularis and orbitalis, and bilateral TPJ (Chan et al., 2004; Klepousniotou et al., 2014; Newman & Joanisse, 2011) divided into its three constituent sub regions: IPL, SMG, and angular gyrus (AG).

Our prediction for Phase 1, when no context is presented, is that competition and selection processes in heterophones would involve mainly phonological representations. This prediction is based on the assumption that the phonological processing of written words is rapid and automatic and may have precedence over semantic processing (Frost, 1998; Ziegler & Goswami, 2005) especially in the LH (Peleg et al., 2012; Peleg & Eviatar, 2008, 2009, 2012; Zaidel & Peters, 1981). Furthermore, because phonological processes are left lateralized (Hickok & Poeppel, 2007; Vigneau et al., 2011) we expect greater activation for heterophones compared to homophones in LH phonological areas. In particular, in the comparison of heterophones and homophones in Phase 1 heterophones are expected to show more activation in left IFG pars opercularis, which has been associated with phonological segmentation (Bitan, Manor, Morocz, & Karni, 2005; Poldrack et al., 1999; Vigneau et al., 2006; Wheat, Cornelissen, Frost, & Hansen, 2010) and left SMG and left IPL, which are implicated in mapping orthography to phonology (Bitan et al., 2007; Hartwigsen et al., 2010; Price, 2012). The selection of one phonological representation in heterophones is expected to reduce the competition among semantic representations as compared to homophones in which the conflict involves *only* semantic representations. Therefore, we expect to find more activation in homophones compared to heterophones in bilateral IFG pars orbitalis and pars triangularis, associated with lexical and semantic retrieval and selection (Moss et al., 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Vigneau et al., 2006) and bilateral angular gyrus implicated in mapping orthography to lexical semantic representations (Binder et al., 2003; Démonet, Thierry, & Cardebat, 2005; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Price, 2000; Seghier, 2013).

In Phase 2, after the presentation of the context, we expect greater activation for the subordinate compared to the dominant meaning, for all ambiguous words, due to the greater effort required for reanalysis of a subordinate-related target if the dominant meaning has been selected in Phase 1. However, this differential activation is expected to show up in different regions and to different extents for homophones and heterophones. In particular, based on the DVF studies described above (Peleg et al., 2012; Peleg & Eviatar, 2008, 2009, 2012) it is expected that heterophones, compared to homophones, will induce a greater commitment toward the dominant meaning, and lower probability of activating the subordinate meaning before the context is presented, resulting in a larger difference between the dominant and subordinate meanings in Phase 2. This is expected specifically in regions involved in mapping orthography to phonology, that is, the LIFG pars opercularis, left IPL, and left SMG. In contrast, in homophones, we expect there to be less need for reanalysis or reactivation when the subordinate context is presented, because it has already been activated earlier, so the difference between the subordinate and dominant meanings will be smaller compared to heterophones and is mainly expected in regions associated with mapping of orthography to semantics, that is, bilateral triangularis, orbitalis and the angular gyri.

Method

Participants

Twenty-four adult native Hebrew speakers, ages 24–35 (*M* = 28.32, *SD* = 2.68) were recruited from university students and their acquaintances. One participant was excluded due to technical problems during data acquisition, resulting in 23 participants in the analysis (13 men, 10 women). All of them were right-handed (Edinburgh Inventory: *M* = 95.65, *SD* = 6.45) with normal or corrected to normal vision, without neurological diseases, psychiatric disorders or language disabilities. One hundred seventy additional participants, from the same population, were recruited for the pretests for the development of the stimuli.

Stimuli

The stimuli consisted of 176 noun–noun homographs: (88 homophones and 88 heterophones) and 66 unambiguous nouns that served as baseline. The ambiguous and unambiguous words were paired with target words that were always unambiguous and were either semantically related or unrelated to the first word. Target words related to ambiguous words were either related to the dominant or to the subordinate meaning of the ambiguous word, while target word related to unambiguous words were related to the only meaning of these words, resulting in a different total number of trials for ambiguous and unambiguous words. One quarter of the ambiguous words and one third of the unambiguous words were not paired with a target word and formed partial trials (see fMRI acquisition section). Altogether the experimental stimuli consisted of 22 trials of each condition, for a total of 242 trials (see examples in Table 1, and the full stimuli set in the online supplementary material Appendices 1 And 2). Similar numbers of trials per condition yielded sufficient power in previous studies of visual word recognition (Bitan et al., 2007; Bitan, Lifshitz, Breznitz, & Booth, 2010; Gennari, MacDonald, Postle, & Seidenberg, 2007; Waldie, Haigh, Badzakova-Trajkov, Buckley, & Kirk, 2013). Homographs were selected from the *Even-Shoshan Hebrew Dictionary* and were balanced across conditions for frequency, polarity, and semantic relatedness to the target word based on the following pretests:

Meaning salience and polarity pretests. To determine which meaning is more dominant (meaning salience) for each homograph, and the distance in salience between the first two meanings (polarity), two pretest were performed. In the first pretest, 20 participants were presented with homographs and their paraphrased meanings and were instructed to indicate the frequency of each one of the meanings of a given homograph on a 1–10 scale. The average score of each meaning across participants multiplied by 10 served as the salience score for that meaning in Pretest 1. In Pretest 2, 20 different participants were presented with the homograph and were instructed to write down their first association of that word. On the next screen, the different meanings of the homograph were presented and participants had to ascribe their association to the most appropriate meaning. The percentage of participants that selected each meaning served as the salience score for that meaning in Pretest 2. A combined salience score was computed for each meaning as the average score from Pretests 1 and 2. For each homograph, the meaning with the highest and second highest salience scores were identified, and these served as the dominant and subordinate meanings, respectively. Homographs were excluded if one or both of the two most salient meanings was not a noun, or if they had more than two meanings with a similar salience score. The difference between the salience scores of the two selected meanings served as the polarity index,[2] which was balanced across all conditions.

Semantic relatedness pretest. To balance the strength of semantic relatedness between the first word in each pair and its target words across ambiguous and unambiguous pairs this pretest presented each homograph or unambiguous word with four related target words, on which 20 participants made a semantic relatedness judgment on a scale of 0–9. For homographs two of these target words were related to its dominant meaning and two were related to the subordinate meaning. The words with the highest score were selected for related pairs and semantic relatedness scores were balanced across all conditions.

Frequency pretest. Finally, to balance the frequency of words in all conditions, all words selected in previous pretests were included in frequency judgment questionnaire administered to 90 participants.

The lists of stimuli for each condition were selected as to balance all of the above factors, as well as the number of gerunds across conditions. There was no significant difference between heterophones and homophones in their polarity (heterophones: *M* = 40.92, *SD* = 22.73; homophones: *M* = 37.60, *SD* = 21.69, *t*[174] = 0.99, *p* = .323), and there were no significant differences between heterophones, homophones, and unambiguous words in their relatedness to the related targets (heterophones: *M* = 4.87, *SD* = 3.30; homophones: *M* = 4.89, *SD* = 3.23; unambiguous: *M* = 3.71, *SD* = 3.33; *F*[2, 176] = 2.144, *p* = .120), and their frequency (heterophones: *M* = 7.33, *SD* = 0.94; homophones: *M* = 7.14, *SD* = 1.05; unambiguous: *M* = 7.23, *SD* = 1.08; *F*[2, 241] = 0.73, *p* = .483). However, there was a significant difference between the number of letters in ambiguous (heterophones and homophones) and unambiguous words (heterophones: *M* = 3.65, *SD* = 0.94; homophones: *M* = 3.74, *SD* = 1.01; unambiguous: *M* = 4.55, *SD* = 0.98; *F*[2, 241] = 18.511, *p* = .001). Unambiguous words had on average 0.5 consonants and 0.4 vowel letters more than heterophones and 0.6 consonants and 0.2 vowel letters more than homophones. Importantly, there was not difference between heterophones and homophones in the number of letters (*p* = .81).

Target words did not differ in frequency between target words of heterophones, homophones and unambiguous words (heterophones targets: *M* = 7.09, *SD* = 1.17; homophones targets: *M* = 7.28, *SD* = 1.12; unambiguous targets: *M* = 7.02, *SD* = 0.99; *F*[2, 176] = 0.885, *p* = .415). Finally, the number of letters in target words was not different between target words of hetereophones: *M* = 4.52, *SD* = 0.996; target words of homophones: *M* = 4.64,

---

[2] For example, for a given homograph if meaning A had a score of 10 in Pretest 1, and a score of 15 in Pretest 2, and meaning B had a score of 80 in Pretest 1 and a score of 70 in Pretest 2, then the polarity index of this homographs was (80 + 70)/2-(10 + 15)/2 = 62.5.

Table 1
Stimuli and Design: Hypothetical English Examples and Number of Items in Experimental Condition

	Ambiguous words		
1st word	Homophones *bank*	Heterophones *tear*	Unambiguous words *beach*
Target word			
Related	To dominant meaning (HomDom) *money* ($n = 22$)	To dominant meaning (HetDom)	*sea* ($n = 22$) *eye* ($n = 22$)
	To subordinate meaning (HomSub) *river* ($n = 22$)	To subordinate meaning (HetSub) *rip* ($n = 22$)	
Unrelated	*cat* ($n = 22$)	*chair* ($n = 22$)	*tree* ($n = 22$)
No target word (partial trial)	— ($n = 22$)	— ($n = 22$)	— ($n = 22$)
Total n	$n = 88$	$n = 88$	$n = 66$

Note. The full stimuli set is presented in the online supplementary materials. HomDom = homophones-dominant; HetDom = heterophones-dominant. HomSub = homophes-subordinate; HetSub = heterophones-subordinate.

$SD = 1.03$; and target words of unambiguous words: $M = 4.62$, $SD = 1.05$; $F[2, 176] = 0.266$, $p = .767$.

Experimental Design and Procedure

To induce full semantic processing of ambiguous words we used a semantic relatedness judgment task during scanning. Each trial began with a 300-ms presentation of a fixation cross followed by the presentation of the first word (ambiguous or unambiguous) in the center of screen for 1,000 ms. After a 2,700-ms interval, the unambiguous target word was presented in 75% of trials with ambiguous words, and in 66% of trials with unambiguous words. The target word was presented centrally for 1,000 ms, followed by a question mark for 2,000 ms, to signal a response was required. Participants indicated whether the two words were related or not by pressing a button with the index or middle finger of their right hand, respectively. This was followed by an intertrial interval of 1,000 ms with additional jitter of 2–6 s (Ollinger, Shulman, et al., 2001).

To enable the orthogonal estimation of activation during the first and second phase of each trial, 22 partial trials (trials with no target word; i.e., no Phase 2) were included in each of the three conditions of Phase 1: heterophones, homophones and unambiguous words. These trials comprise 25% of heterophones and homophones and 33% of unambiguous words (the difference is due to a different total number of trials between ambiguous and unambiguous words). Partial trials have been developed as a way to separate the estimated blood oxygenation level-dependent (BOLD) signal from two phases in compound trials, in which full randomization of the order of the first and second events in the trial is not possible (Ollinger, Shulman, et al., 2001). In this design, it is critically important that participants are unable to predict whether a trial is going to be a full or a partial trial. Mixing the partial and full trials increases the likelihood that most of the cognitive processes during a partial trial are the same as those during the first component of a compound trial. The interval between successive trials of either type is randomly varied. Simulation have shown that this method is superior to introduction of variable long spacing within trials (Ruge, Goschke, & Braver, 2009), and that including 20–33% of partial trials yields accurate estimates of the separate BOLD signal in the two phases (Ollinger, Corbetta, & Shulman, 2001). This method has been used in studies of attention (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006; Woldorff et al., 2004), working memory (Bennett, Rivera, & Rypma, 2013) and language processing (Meltzer, McArdle, Schafer, & Braun, 2010). Partial trials in the current study consisted of the first 4,000 ms of the full trial (300-ms fixation cross, 1,000-ms first word presentation, and 2,700-ms blank screen; see Figure 1). Thus, because target words appear in the majority of the trials, and participants do not know in advance which trials are partial trials and which are full trials, processing of the first word during the first 4,000 ms of the trial is expected to be similar across partial and full trials. However, any additional processing (such as reactivation) of the first word which are triggered by the presentation of the target word will be captured by the analysis of the second phase.

The total of 242 trials (176 full compound trials, 66 partial trials) were pseudorandomly intermixed in an event-related design using OptSeq2 (see www.surfer.nmr.mgh.harvard.edu/

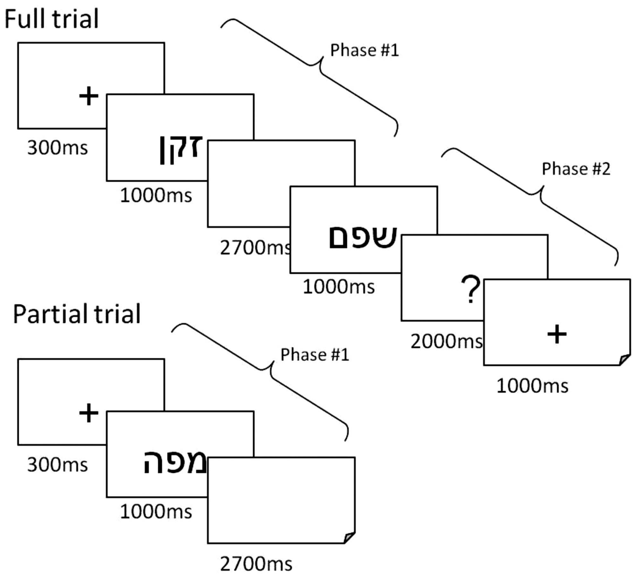

Figure 1. Time course of experiment. Phase 1 in the partial trial and in full trial have identical structures.

optseq; Dale, 1999). These were divided into four runs: two runs of 580 s (9.67 min) and two runs of 484 s (8.07 min). The order of runs was counter balanced across participants.

Data Acquisition

fMRI scans were acquired at the Functional Brain Imaging Center, in Tel-Aviv Sourasky Medical Center, using a 3.0 Tesla GE Signa EXCITE scanner with eight-channel receive-only head coil. The stimuli were projected using an EPSON back-projection onto a screen, and viewed through a mirror attached to the inside of the head coil. Participants' responses were recorded using a four-button "Current Designs" optical response box. A susceptibility weighted single-shot EPI (echo planar imaging) method with BOLD was used. Twenty-six slices were acquired in a sequential ascending order (from bottom to top) with the following scan parameters: TE (Time to Echo) = 35 ms, flip angle = 78, matrix size = 96 × 96, field of view = 38.4 cm, slice thickness = 3 mm (+1 mm gap), TR (Time to Repeat) = 2000 ms. Two runs of 290 images and two runs of 242 images each were acquired. In addition, a high resolution, anatomical T1 weighted 3D structural images were acquired (TR = 9.044 ms, TE = 3.0504 ms, flip angle = 13°, matrix size = 256 × 256, field of view = 25.6 cm, slice thickness = 1 mm) using an identical orientation as the functional images.

fMRI Data Preprocessing and Statistical Analysis

Data analysis was done using the Statistical Parametric Mapping software in Matlab (SPM8-Welcome Trust Centre for Neuroimaging, University College London, www.fil.ion.ucl.ac.uk/spm). The images were spatially realigned to the first volume in each run to correct for head movements. Average movement per run was 0.76 mm (movement in one participant was 3.98 mm, and the rest were <2.6 mm). Because interpolation was used to minimize timing errors between slices (Henson, Buechel, Josephs, & Friston, 1999). The functional images were coregistered with the anatomical image, and normalized to the standard T1 template volume (MNI). Normalized images were resampled with isotropic voxels of 2 × 2 × 2 mm and the data were then smoothed with a 7-mm isotropic Gaussian kernel, which is more than 3 times the size of the voxels, and thus increases the statistical power but still enables appropriately high resolution to distinguish between adjacent cortical areas.

Statistical analyses at the first level was conducted using an event-related design with a high-pass filter with a cutoff period of 128 s for trials with correct responses only. The BOLD signal was convolved with the canonical hemodynamic response function, and AR(1) correction was applied. The analysis separately modeled the first and second phases of each trial and thus included 11 conditions. The first phase of each trial was defined as one of three conditions according to the identity of the first word: heterophones (88 trials), homophones (88 trials), or unambiguous words (66 trials). The second phase of each trial was categorized into one of 8 conditions according to the target word (with 22 trials in each condition): heterophone-dominant (HetDom—a target word related to the dominant meaning of a heterophone); heterophone-subordinate (HetSub); heterophone-unrelated (HetUnrel); homophones-dominant (HomDom); homophone-subordinate (HomSub); homophone-unrelated (HomUnrel); unambiguous-related (UnambigRel); and unambiguous-unrelated (UnambigUnrel).

Whole brain group analyses were conducted separately for each phase using the flexible factorial design in SPM. Individual contrasts comparing each condition to the mean were taken into the group analysis. For Phase 1, the model included individual contrasts from all three conditions (homophones, heterophones and unambiguous words). This was used to look at the group activation across all conditions of Phase 1 (Figure 3a and Table 2) and to directly compare between homophones and heterophones (results not shown as there were no significant clusters). For Phase 2, the model included individual contrasts from all 8 conditions, and was used to look at overall activation across all conditions (Figure 3b and Table 2) and to compare the subordinate with the dominant meanings for each type of homograph (see Table 3). Further in-depth analyses of these effects were conducted using an ROI analysis approach.

ROI analysis. ROI analysis was conducted in bilateral IFG and TPJ in order to directly compare among regions and hemispheres. Anatomical ROIs within these cortical areas were defined based on the Anatomical Atlas Labeling (AAL) from the WFU Pickatlas for SPM (Maldjian, Laurienti, Kraft, & Burdette, 2003). For IFG these include pars opercularis (OPER), pars triangularis (TRI), and pars orbitalis (ORB). For TPJ, these include SMGs, AGs, and IPL. Activation in these ROIs was calculated separately given evidence for their involvement in distinct aspects of reading: for example, phonological segmentation and phonological decoding of written words (OPER; Bitan, Manor, et al., 2005; Poldrack et al., 1999; Vigneau et al., 2006; Wheat et al., 2010); lexical/semantic retrieval and selection (TRI and ORB; Moss et al., 2005; Thompson-Schill et al., 1997; Vigneau et al., 2006), mapping of orthography to phonology (SMG and IPL; Bitan et al., 2007; Graves et al., 2010; Hartwigsen et al., 2010; Price, 2012); and mapping of orthography to semantics (AG; Graves et al., 2010; Seghier, 2013). All regions were selected in the two hemispheres to test the lateralization of processing ambiguous words (Jung-Beeman, 2005; Peleg & Eviatar, 2009).

Changes in signal intensity during each phase were extracted using the MarsBaR toolbox for SPM (MARSeille Boîte À Région *d'*Intérêt, v.0.43; Brett, Anton, Valabregue, & Poline, 2002). For each participant, percent signal change was calculated comparing each ambiguous condition to the corresponding unambiguous condition as a measure of the effect of ambiguity. For Phase 1, this resulted in two contrasts: heterophone versus unambiguous and homophone versus unambiguous. For Phase 2, we extracted four contrasts comparing target words related to each type of homograph to target words related to unambiguous words: HetDom versus UnambigRel; HetSub versus UnambigRel; HomDom versus UnambigRel; and HomSub versus UnambigRel.'For comparison with previous studies we first tested whether there was a significant effect of ambiguity in our regions of interest. This was done by comparing the signal change in each of the contrasts described above, in each ROI, to zero in a one sample t test. The results are reported at a threshold of $p < 0.05$ following Bonferroni correction for multiple comparisons (12 ROIs). To examine our main hypotheses General Linear model (GLM) repeated measures analyses were then conducted separately for IFG and TPJ. For Phase 1, the model included three within-subject factors: 3 ROIs × 2 hemispheres × 2 levels of phonological disparity (heterophones

Table 2

Regions of Activation in Whole Brain Analysis for All (Ambiguous and Unambiguous) Words in Phase 1 and All Words in Phase 2, at familywise error (FWE) corrected p < .05, Cluster Size > 10 Voxels

Region	Hemisphere	BA	Cluster size (voxels)	Peak Z value	x y z
All words in Phase 1					
Mid. occipital/fusiform/lingual gyri	L	19/18	1,213	6.71	−40 −86 −10
Inf. occipital/inf. temporal	R	19	854	6.54	40 −84 −10
Angular	R	7	99	5.87	3 −62 48
Precentral	L	6	106	5.81	−42 0 38
All target words in Phase 2					
Insula	R	13	454	7.23	32 24 0
Fusiform/lingual gyri	L	18/37	1,136	7.19	−46 −64 −18
Insula/inf. frontal gyrus opercularis, triangularis	L	44	1,770	7.04	−32 22 0
Postcentral gyrus/inf. parietal lobule	L	40	885	6.91	−48 −30 48
Thalamus	L		1,235	6.89	−6 −26 −10
Supplementary motor area/mid cingulate/sup. medial frontal	L	32	1,115	6.88	−6 10 46
Inf. occipital/fusiform gyri/cerebellum	R	18/37	817	6.78	38 −86 −8
Sup. parietal lobule	R	40	124	6.52	32 −62 50
Sup. frontal gyrus	L	6	59	6.14	−24 −10 50
Precentral/Inf. frontal gyrus opercularis	R	9	150	5.78	58 6 32
Supramarginal gyrus	R	40	95	5.52	36 −38 44
Inf. parietal lobule	L	40	115	5.46	−26 −68 42
Globus pallidus/putamen	L		115	5.45	−18 6 0
Precentral gyrus	R	6	35	5.39	32 −2 50

Note. Inf. = inferior; sup. = superior; R = right; L = left.

and homophones). To follow up on the interaction between phonological disparity ROI and hemisphere and to test our hypotheses about the differences between heterophones and homophones, we then computed the difference between heterophones and homophones and used it as the dependent variable in follow-up analyses. For Phase 2, the initial GLM analyses included four within-subject factors: 3 ROIs × 2 hemispheres × 2 phonological disparity levels (heterophones or homophones) × 2 meaning salience levels (dominant vs. subordinate). To test the hypothesis that the effect of meaning salience is greater for heterophones, we calculated the difference between subordinate and dominant related target words and used it as the dependent variable in follow-up analyses. For both Phase 1 and Phase 2, because our hypotheses were concerned with both region and hemispheric effects, when interaction between ROI and hemisphere were significant we conducted the follow-up analyses in two ways: (a) separate analyses for each hemisphere, with ROI as a within subject factor, and (b) separate analyses for each ROI with hemisphere as a within subject factor. Post hoc comparisons are presented with Bonferroni correction for multiple comparisons.

Results

Behavioral Results

The effects of ambiguity (responses to ambiguous minus unambiguous words) on accuracy (as measured by percent of errors) and response time (as measured by mean across participants' median reaction time [RT] to correct responses) are shown in Figure 2. These measures served as the dependent variables in repeated measures ANOVAs that were conducted for related pairs ("yes" responses) with two independent variables: phonological disparity (heterophone or homophone) and the salience of the meaning to which the target word was related (dominant or subordinate meaning). We found a significant main effect of salience in both measures: errors, $F(1, 22) =$

Table 3

Regions of Activation in Whole Brain Analysis for the Comparison of the Subordinate and Dominant Meanings in Phase 2, at p < .05 FWE corrected, Cluster Size > 10 Voxels

Region	Hemisphere	BA	Cluster size (voxels)	Peak Z value	x y z
HetSub-HetDom					
Inferior frontal gyrus pars triangularis	L	46	77	5.08	−46 20 28
Middle temporal gyrus	L	21	10	5.07	−48 −32 −4
Inferior frontal gyrus pars opercularis/precentral	L	6	34	4.97	−40 4 28
Inferior frontal gyrus para orbitalis	L	47	14	4.84	−44 42 −6
HomSub-HomDom					
NA					

Note. HetSub = heterophone-subordinate; HomDom = homophones-dominant; HomSub = homophone-subordinate; HetDom = heterophones-dominant.

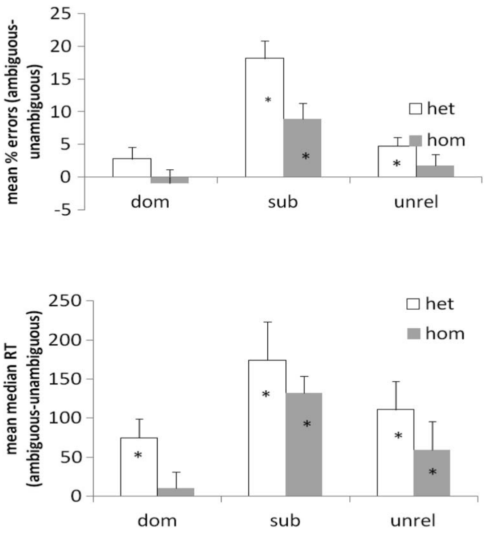

Figure 2. Magnitude of ambiguity effects for accuracy (mean % errors ambiguous − unambiguous) and for response time (mean median RT ambiguous − unambiguous) of semantic judgment task during scanning. Asterisk indicates a significant one-sample *t* test for the column. RT = response time; het = heterophones; hom = homophones; dom = dominant; sub = subordinate; unrel = unrelated. Dom and Sub represent "yes" responses, whereas unrelated represents "no" responses. * $p < 0.01$.

82.63, $p < .0001$, and RT, $F(1, 22) = 20.76$, $p < .0005$, showing that the ambiguity effect was larger for the subordinate compared to the dominant meanings. We also found a larger ambiguity effect for heterophones than for homophones, significant in errors, $F(1, 22) = 24.14$, $p < .0001$.

For the unrelated pairs ("no" responses), as shown in Figure 2, the ambiguity effect was significant for heterophones in both errors and median RT—accuracy: $t(22) = 3.58$, $p < .005$; RT: $t(22) = 3.15$, $p < .005$—and not for homophones.

Imaging Results

The results of a whole brain analysis for all (ambiguous and unambiguous) words in Phase 1 and for all target words in Phase 2 show activation in expected regions of the language network associated with word reading (see Figure 3 and Table 2). A direct comparison between heterophones and homophones in Phase 1 did not show any significant clusters of activation after family wise error correction at the level of the whole brain ($p < 0.05$ FWE correction, extent >10). A direct comparison between subordinate and dominant meanings in Phase 2 showed significant clusters of activation ($p < 0.05$ FWE correction, extent >10) only for heterophones. These clusters were found in LIFG (pars triangularis, opercularis and orbitalis), and in left middle temporal gyrus (see Table 3). These effects were further examined in ROI analyses.

Reading Homographs (Phase 1)

Frontal regions. Figure 4 shows the ambiguity effect (percent signal change in ambiguous vs. unambiguous words) separately for heterophones > unambiguous and homophones > unambiguous in each ROI in IFG. No regions showed significant activation compared to unambiguous words at the corrected *p* level. To compare between homophones and heterophones a GLM repeated measures analysis of regions in IFG was conducted with ROI, hemisphere and phonological disparity, as within subject factors. This analysis showed a significant main effect for hemisphere, $F(1, 22) = 6.62$, $p < 0.05$, $\eta_p^2 = 0.23$, with greater activation on the left. There was also a significant interaction of ROI and phonological disparity, $F(2, 44) = 50.42$, $p < 0.001$, $\eta_p^2 = 0.70$, and a three-way interaction of ROI, hemisphere, and phonological disparity, $F(2, 44) = 4.92$, $p < 0.05$, $\eta_p^2 = 0.18$. To test our predictions that the difference between heterophones and homophones involves regions associated with phonological processing, we performed follow-up analyses on the difference between heterophones and homophones (phonological disparity) as the dependent variable, separately for each hemisphere, with ROI as a within subject factor.

These analyses showed a significant effect of ROI in the LH, $F(2, 44) = 55.57$, $p < 0.001$, $\eta_p^2 = 0.72$, with pairwise comparisons showing significantly greater phonological disparity effect in OPER > TRI ($p < 0.001$) and TRI > ORB ($p < 0.001$). The signal in left opercularis was greater for heterophones than homophones, $t(22) = 3.48$, $p < 0.01$, whereas activation in left orbitalis was greater for homophones compared to heterophones, $t(22) = 2.2$, $p < 0.05$. The effect of ROI was also significant in the RHs, $F(2, 44) = 11.33$, $p < 0.001$, $\eta_p^2 = 0.34$, with pairwise comparisons showing a significant difference between orbitalis on the one hand compared to both opercularis ($p < 0.01$) and triangularis ($p < 0.01$) on the other. The signal in right orbitalis was greater for homophones compared to heterophones, $t(22) = 3.01$, $p < 0.01$ (see Figure 4). To test our prediction that effects of phonological disparity are primarily found in the LH we also conducted a separate *t* test within each ROI, comparing between hemispheres, with the difference between heterophones and homophones as the dependent measure. Only the opercularis showed a significant difference between hemispheres, $t(22) = 2.94$, $p < 0.01$, with a

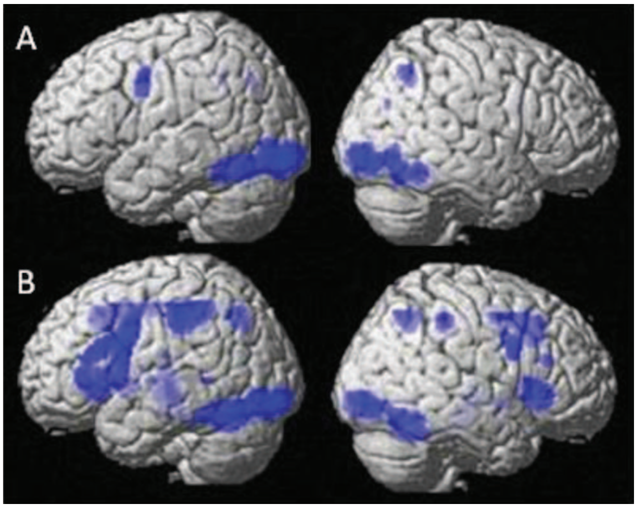

Figure 3. Whole brain analysis for all ambiguous and unambiguous words in Phase 1 (A) and all target words in Phase 2 (B). familywise error (FWE) corrected $p < 0.05$ cluster size >10 voxels. See the online article for the color version of this figure.

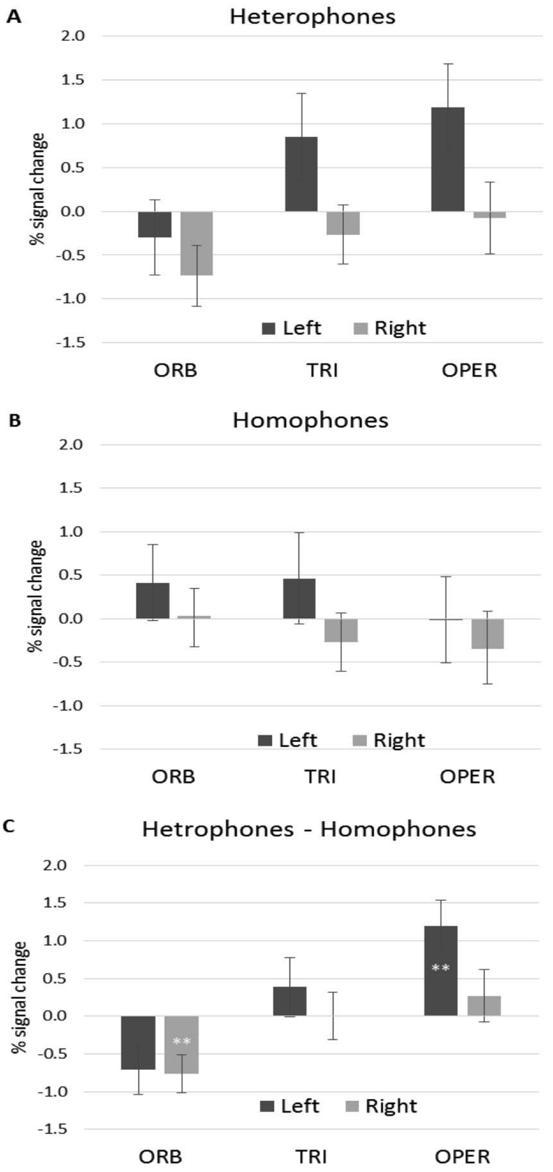

Figure 4. Signal change during homograph presentation (Phase 1) in inferior frontal gyrus regions of interest: Ambiguity effects for heterophones (A) and homophones (B) versus unambiguous words; (C) differences between heterophones and homophones. ** indicate effects significantly different from zero at $p < 0.05$ corrected for multiple comparisons. Bars indicate *SE*. ORB = orbitalis; TRI = triangularis; OPR = opercularis.

larger effect in the LH. To summarize, the effects in IFG, we found a larger ambiguity effect for heterophones than for homophones in left OPER, and a larger ambiguity effect for homophones compared to heterophones in bilateral Orb. The effect of phonological disparity in OPER was stronger in the left compared to the RH.

Temporo-parietal regions. Figure 5 shows the ambiguity effect in the TPJ. One sample *t*-tests show that heterophones presentation resulted in significantly reduced activation compared to unambiguous words in left AG, $t(22) = 4.33$, and right IPL, $t(22) = 3.32$, corrected $p < 0.05$. The ambiguity effect in homophones was not significant at the corrected level. GLM repeated measures analysis with ROI, hemisphere and phonological disparity as within-subject factors revealed a significant interaction of ROI and phonological disparity, $F(2, 44) = 7.81$, $p < 0.01$, $\eta_p^2 = 0.26$, and of ROI, hemisphere, and phonological disparity, $F(2, 44) = 17.69$, $p < 0.001$, $\eta_p^2 = 0.45$. To test which regions show an effect of phonological disparity, follow-up analysis were conducted with phonological disparity as the difference between heterophones and homophones in each ROI as the dependent variable in a separate GLM analysis for each hemisphere with ROI as a within subject factor.

This analysis showed a significant effect of ROI only in the LH ($F(2, 44) = 18.39$, $p < 0.001$, $\eta_p^2 = 0.46$). Pairwise comparisons of phonological disparity effects between ROIs showed a significant difference between AG on the one hand and both SMG ($p <$

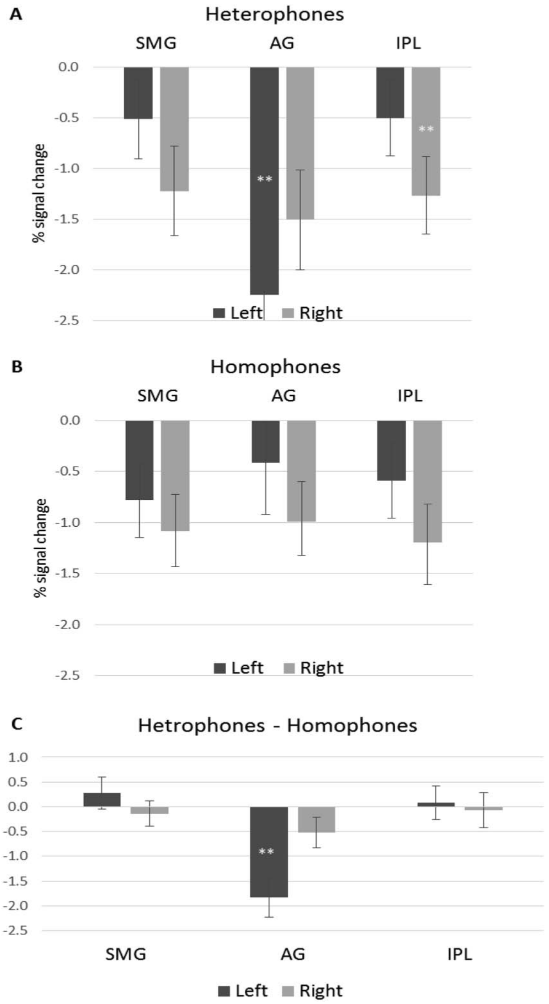

Figure 5. Signal change during homograph presentation (Phase 1) in temporo-parietal junction (TPJ) regions of interest. Ambiguity effects for heterophones (A) and homophones (B) versus unambiguous words. (C) Differences between heterophones and homophones. ** indicate effects significantly different from zero at $p < 0.05$ corrected for multiple comparisons. Bars indicate *SE*. SMG = supramarginal gyrus; AG = angular gyrus; IPL = inferior parietal lobule.

0.01) and IPL ($p < 0.001$) on the other. Activation in left AG was significantly lower in heterophones compared to homophones, $t(22) = 3.73$, $p < 0.01$, whereas no effect of phonological disparity was found in the other regions. To test our prediction that effects of phonological disparity are primarily found in the LH we also conducted a separate t test within each ROI, comparing between hemispheres, with the difference between heterophones and homophones as the dependent measure. Only the AG showed a significant difference between hemispheres, $t(22) = 4.08$, $p < 0.0001$) with a larger effect in the LH. To summarize, the effects in TPJ, we found a negative ambiguity effect for heterophones in left AG and right IPL. Activation in left AG was significantly lower for heterophones compared to homophones, and this difference was larger in the left compared to the RH.

Figure 6 summarizes the ROIs showing a significant difference between heterophones and homophones in Phase 1.

Integrating Homographs With the Context (Phase 2)

Recall that all of the target words here were unambiguous, and they differed in whether they followed ambiguous or unambiguous words, and whether they were related to the more frequent (dominant) or less frequent (subordinate) meaning of the homographs.

Frontal regions. Figure 7 shows the ambiguity effects in each ROI in IFG, for target words related to the subordinate or dominant meanings of heterophones or homophones, compared to target words related to unambiguous words. This figure shows a positive ambiguity effect for subordinate related meanings of both types of ambiguous words—one sample t tests were significant for heterophones (HetSub) in all LH regions (L-ORB: $t(21) = 4.38$; L-TRI: $t(22) = 4.98$; L-OPR: $t(22) = 4.53$, corrected $p < 0.05$) and for homophones (HomSub) in bilateral OPR (LH: $t(22) = 4.96$, RH: $t(22) = 3.2$, corrected $p < 0.05$) and bilateral TRI (LH: $t(22) = 4.75$, RH: $t(22) = 3.30$, corrected $p < 0.05$). In contrast, target words related to the dominant meanings showed a different pattern. For heterophones, dominant related target words (HetDom) showed a negative ambiguity effect (reduced activation compared to target words related to unambiguous words; significant in all regions except right ORB—L-ORB: $t(22) = 3.54$; L-TRI: $t(22) = 6.90$; R-TRI: $t(22) = 4.0$; L-OPR: $t(22) = 8.73$; R-OPR: $t(22) = 5.72$, corrected $p < 0.05$. No ambiguity effect was found for HomDom. GLM repeated measures analysis was performed on

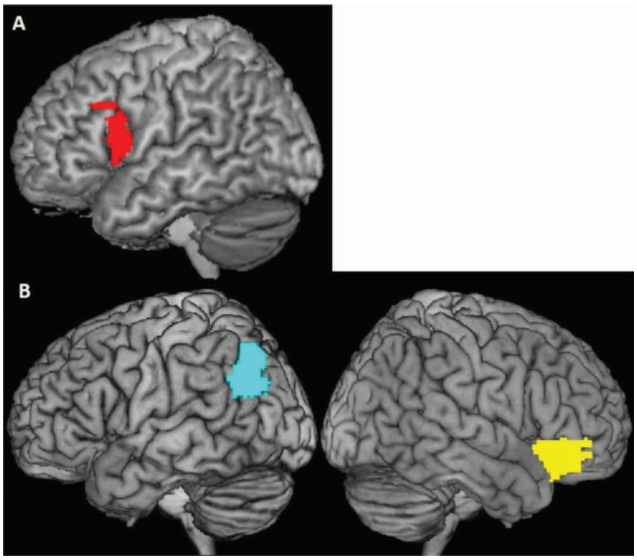

Figure 6. Regions of interest showing a significant effect of phonological disparity. A: Greater activation in heterophones > homophones in left inferior frontal gyrus (IFG) pars opercularis (in red/ darkest grey); B: Greater activation in homophones > heterophones (due to reduced activation in heterophones) in left angular gyrus (cyan/ middle grey) and right IFG pars orbitalis (yellow/ birghtest grey). See the online article for the color version of this figure.

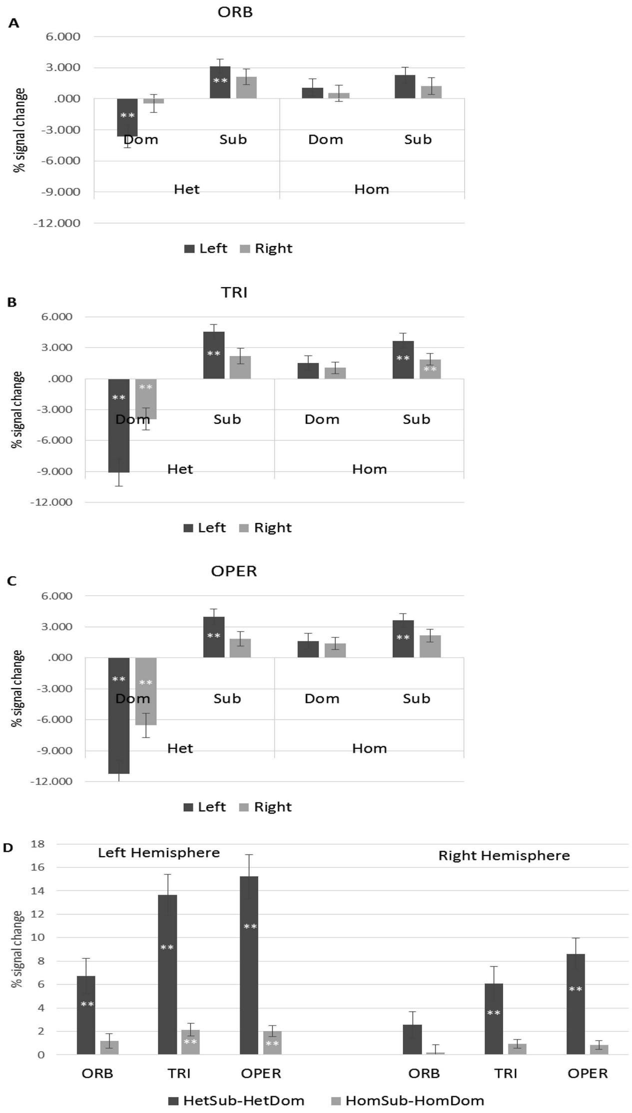

Figure 7. Signal change during integration of the homograph with the context (Phase #2) in inferior frontal gyrus regions of interest. The ambiguity effects for target words related to the dominant (Dom) and subordinate (Sub) meaning of ambiguous words versus target words related to unambiguous words in (A) orbitalis, (B) triangularis, and (C) opercularis. D: The effect of meaning salience (Sub-Dom) for all regions. ** indicate effects significantly different from zero at $p < 0.05$ corrected for multiple comparisons. Bars indicate *SE*. Het = heterophones; Hom = homophones.

IFG regions, with ROI, hemisphere, phonological disparity and meaning salience as within subject factors. This analysis showed significant three way interactions of ROI × Hemisphere × Meaning Salience, $F(2, 42) = 4.09$, $p < 0.05$, $\eta_p^2 = 0.16$, and of ROI × Phonological Disparity × Meaning Salience, $F(2, 42) = 22.23$, $p < 0.001$, $\eta_p^2 = 0.51$.

To test our predictions that the difference between subordinate and dominant meaning are greater in heterophones compared to homophones in regions associated with phonological processing we used the difference between the subordinate and dominant meanings as the dependent variable in the follow up analyses. We first conducted a separate GLM analyses within each hemisphere, with ROI, and phonological disparity as within subject factors. For both hemispheres there was a significant effect of ROI, $F(2, 44) = 30.8$, $p < 0.001$, $\eta_p^2 = 0.60$, $F(2, 44) = 11.84$, $p < 0.001$, $\eta_p^2 = 0.35$, for the LHs and RHs, respectively, showing greater effects of meaning salience in OPR and TRI compared to ORB ($p < 0.01$). There was also a significant effect of phonological disparity, $F(1, 22) = 40.27$, $p < 0.001$, $\eta_p^2 = 0.66$; $F(1, 22) = 20.51$, $p < 0.001$, $\eta_p^2 = 0.48$, for the LHs and RHs, respectively, showing greater effects of meaning salience in heterophones, and a significant interaction of phonological disparity and ROI, $F(2, 44) = 18.2$, $p < 0.001$ $\eta_p^2 = 0.46$; $F(2, 44) = 12.11$, $p < 0.001$, $\eta_p^2 = 0.36$, respectively, in the LHs and RHs. Separate analyses within each ROI show that the effect of phonological disparity was significant for left and right OPER, $t(22) = 6.98, 6.13$, respectively ($p < 0.0001$); left and right TRI, $t(22) = 6.08, 3.67$, respectively ($p < 0.001$), and left ORB, $t(22) = 3.61$, $p < 0.005$. Figure 7d shows that this effect was weaker for ORB in both hemispheres.

To test our prediction of hemispheric differences in the effects of meaning salience we conducted another follow-up analysis within each ROI, with hemisphere and phonological disparity as independent factors, and the difference between subordinate and dominant meanings as the dependent measure. All IFG ROIs showed a significant main effect of hemisphere, indicating that the effect of meaning salience was greater in the left compared to the RH—Orb: $F(1, 21) = 27.91$, $p < 0.001$, $\eta_p^2 = 0.57$; TRI: $F(1, 22) = 18.77$, $p < 0.001$, $\eta_p^2 = 0.46$; Oer: $F(1, 22) = 14.33$, $p < 0.01$, $\eta_p^2 = 0.39$. All ROIs also showed a significant interaction between phonological disparity and hemisphere—Orb: $F(1, 21) = 16.34$, $p < 0.01$, $\eta_p^2 = 0.44$; TRI: $F(1, 22) = 11.86$, $p < 0.01$, $\eta_p^2 = 0.35$; OPER: $F(1, 22) = 11.39$ $p < 0.01$, $\eta_p^2 = 0.34$—showing that the difference between heterophones and homophones was greater in the LH compared to the RH. Altogether the analyses within IFG show that the effects of meaning salience are stronger in heterophones compared to homophones, are stronger in the LH compared to the RH, and are stronger in OPER and TRI compared to Orb. Similarly the effect of phonological disparity is also stronger in the LH and in OPER and TRI.

TPJ. Figure 8 shows the ambiguity effect for target words in TPJ ROIs. One sample *t* tests show that the dominant meaning in heterophones (HetDom) resulted in a significantly reduced activation compared to target words related to unambiguous words in left SMG and left IPL, $t(22) = 3.47$ and 8.39, respectively, corrected $p < 0.05$. A GLM repeated measures analysis was performed across all TPJ regions, with ROI, hemisphere, phonological disparity, and meaning salience as within-subject factors. The four way interaction was significant, $F(2, 42) = 8.65$, $p < 0.01$, $\eta_p^2 = 0.29$.

To test our predictions that the difference between subordinate and dominant meaning are greater in heterophones compared to homophones in regions associated with phonological processing we used the difference between the subordinate and dominant meanings as the dependent variable in the follow up analyses. We first conducted separate GLM analyses within each hemisphere, with ROI, and phonological disparity as within subject factors. These analyses showed a significant effect of ROI within the LH, $F(2, 44) = 33.16$, $p < 0.001$, $\eta_p^2 = 0.61$, with a greater effect in IPL > SMG, and SMG > AG ($p > .001$); and within the RH, $F(2, 44) = 6.27$, $p < 0.01$, $\eta_p^2 = 0.22$, with greater effect in IPL > AG ($p < 0.01$). The effect of phonological disparity was significant only in the LH, $F(1, 21) = 9.63$, $p < 0.01$, $\eta_p^2 = 0.31$, and the interaction between phonological disparity and ROI was significant in both hemispheres, LH: $F(2, 42) = 21.11$, $p < 0.001$, $\eta_p^2 = 0.50$, and RH: $F(2, 44) = 3.56$, $p < 0.05$, $\eta_p^2 = 0.14$. Follow-up analysis showed that the effect of phonological disparity in SMG was only significant in the LH—left SMG, $t(22) = 2.18$, $p < 0.05$—whereas in IPL it was found bilaterally—left IPL: $t(22) = 5.77$, $p < 0.001$; right IPL: $t(22) = 2.32$, $p < 0.05$.

Finally, to test our prediction that effects of meaning salience are stronger in the LH an additional follow-up analysis was carried out, separately within each ROI, with hemisphere, and phonological disparity as within subject factors and the difference between the subordinate and dominant meanings as the dependent measure. No significant effects were found for AG. There were significant effects of hemisphere in SMG, $F(1, 22) = 5.28$, $p < 0.05$, $\eta_p^2 = 0.19$, and in IPL, $F(1, 22) = 30.29$, $p < 0.001$, $\eta_p^2 = 0.58$, with stronger effects of meaning salience in the LH. IPL also showed a significant effect of phonological disparity, $F(1, 22) = 17.84$, $p < 0.001$, $\eta_p^2 = 0.45$, with stronger effects of meaning salience in heterophones compared to homophones. Both SMG and IPL also showed significant interaction of hemisphere and phonological disparity, SMG: $F(1, 22) = 4.81$, $p < 0.05$, $\eta_p^2 = 0.18$; and IPL: $F(1, 22) = 18.49$, $p < 0.001$, $\eta_p^2 = 0.46$).

Altogether the analyses within TPJ show that the effects of meaning salience are stronger in bilateral IPL and left SMG compared to AG. They are also stronger in heterophones compared to homophones in bilateral IPL and left SMG. For IPL the effect of meaning salience is larger in the LH, and the difference between heterophones and homophones is also larger in the LH.

Figure 9 summarizes the ROIs showing a significant difference between the subordinate and the dominant meaning in ambiguous words in Phase 2.

Discussion

Our study examined the effect of ambiguity in homophonic and heterophonic homographs on brain activation in two discrete phases of reading ambiguous words. The first phase is the presentation of the ambiguous word without any context, in which mapping and selection processes may be based only on salience of the words meanings. The second phase is the presentation of the context, in the form of a target word, in which the ambiguous word is integrated with the context, and the ambiguity resolved. We will first consider these two phases separately.

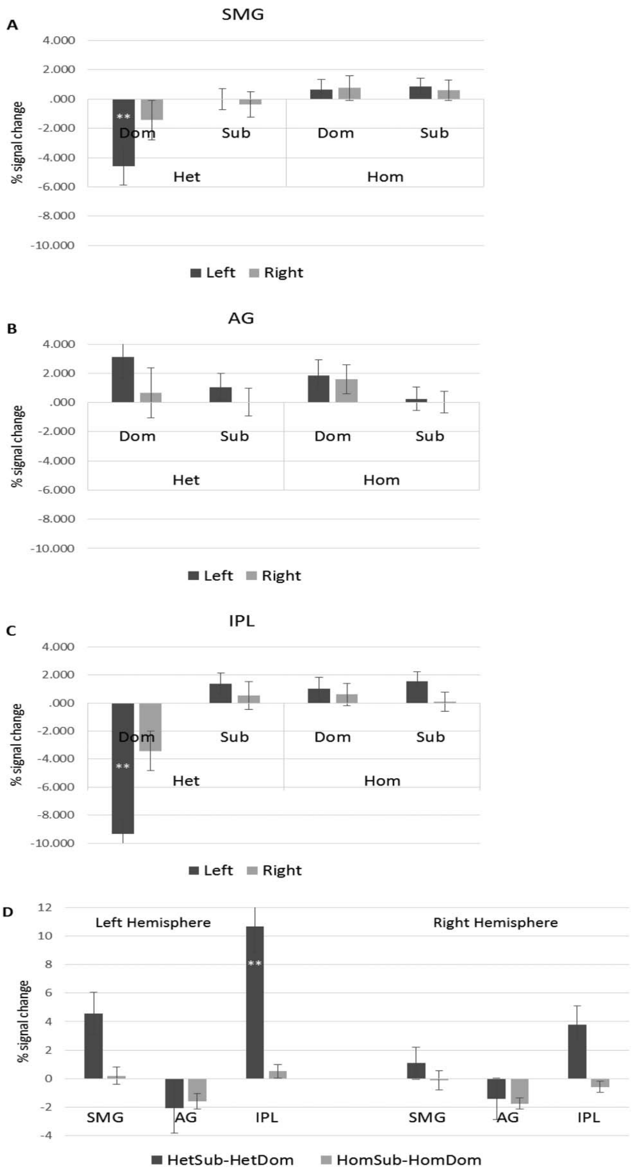

Figure 8. Signal change during integration of the homograph with the context (Phase #2) in temporo-parietal junction (TPJ) regions of interest. The ambiguity effects for target words related to the dominant (Dom) and subordinate (Sub) meaning of ambiguous words versus target words related to unambiguous words in (A) supramarginal gyrus, (B) angular gyrus, and (C) inferior parietal lobule. D: The effect of meaning salience (Sub-Dom). ** indicate effects significantly different from zero at $p < 0.05$ corrected for multiple comparisons. Bars indicate *SE*. Het = heterophones; Hom = homophones.

Phase 1: Reading of Ambiguous Words With no Context

Frontal regions. The presentation of ambiguous words without any context resulted in greater activation for heterophones compared to homophones in left IFG pars opercularis, known to be associated with phonological segmentation and phonological decoding of written words (Bitan, Manor, et al., 2005; Poldrack et al., 1999; Vigneau et al., 2006; Wheat et al., 2010). In contrast, the ambiguity effect in homophones was greater than in heterophones in bilateral IFG pars orbitalis, which has been implicated in lexical-semantic retrieval processes (Moss et al., 2005; Thompson-Schill et al., 1997; Vigneau et al., 2006). These results are consistent with our predictions for Phase 1, of greater activation for heterophones compared to homophones in regions associated with phonological processing, and greater activation in homophones compared to heterophones in regions associated with semantic processing.

Previous neuroimaging studies that targeted the first phase of processing ambiguous words without context pointed to the involvement of anterior and dorsal parts of left IFG, which has been suggested to reflect the conflict and selection processes based on the salience of the lexical representation (Acheson & Hagoort, 2013; Ihara et al., 2007; Rodd et al., 2012; Rodd, Vitello, Woollams, & Adank, 2015). In the current study, the comparison of ambiguous (heterophones and homophones separately) to unambiguous words in bilateral IFG did not survive the correction for multiple comparisons. However, the direct comparison between heterophones and homophones showed a different ambiguity effect in these same regions. Activation for heterophones in left pars operculais may reflect enhanced sublexical decoding to overcome the ambiguous mapping of orthography to phonology. Furthermore, the reduced activation in bilateral pars orbitalis for heterophones compared to homophones suggests that although both types of words are semantically ambiguous, heterophones induce less semantic conflict than homophones. Thus, for heterophones, the resolution of the conflict at the phonological level eliminates the ambiguity from the lexical-semantic level. These findings are consistent with our prediction that competition and selection processes in heterophones involve mainly phonological representations, and indicates a prominent role of phonological decoding, even in a task that does not emphasize phonological processes.

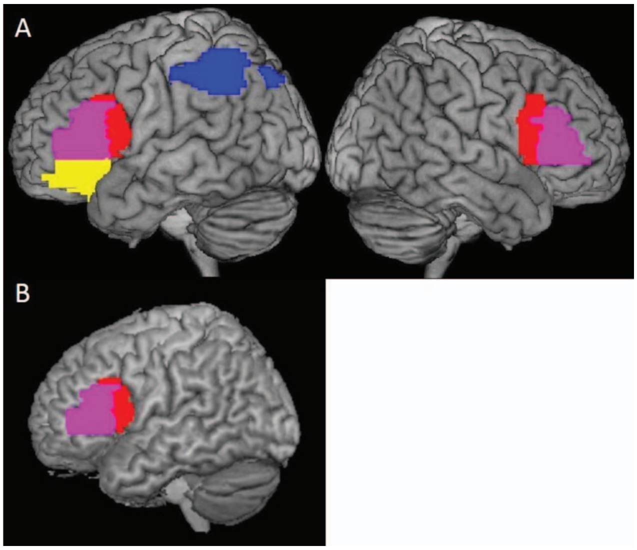

Figure 9. Region of interest showing a significant effect of meaning salience (Sub > Dom) in heterophones (A) and in homophones (B). Inferior frontal gyrus (IFG): pars opercularis (red), pars orbitalis (yellow), pars triangularis (pink); temporo-parietal junction (TPJ): inferior parietal lobule (IPL; blue). See the online article for the color version of this figure.

Also consistent with our prediction is the different patterns of hemispheric lateralization found for heterophones and homophones. While activation in heterophones was left lateralized (opercularis) activation in homophones (compared to heterophones) was bilateral (orbitalis). This pattern of lateralization is consistent with the idea of greater left lateralization of phonological compared to semantic processes in written and oral language (Hickok & Poeppel, 2004; Spironelli & Angrilli, 2006; Vigneau et al., 2011). It is also consistent with the hypothesis that direct mapping of orthography to phonology during reading occurs only in the LH, whereas mapping of orthography to semantic representations occurs bilaterally (Peleg et al., 2012; Peleg & Eviatar, 2008, 2009, 2012).

Temporo-parietal regions. Our results for Phase 1 also showed unexpected negative ambiguity effects (decreased activation in ambiguous compared to unambiguous words) in bilateral TPJ. Specifically this effect was found in left AG and right IPL for heterophones. The difference between heterophones and homophones was only found in the LH, and specifically in left AG, with lower activation for heterophones. Regions in TPJ are typically associated with mapping from orthography to higher representation, with SMG and IPL associated primarily with mapping to phonology (Bitan et al., 2007; Hartwigsen et al., 2010; Price, 2012) and AG with mapping to lexical semantic representations (Binder et al., 2003; Démonet et al., 2005; Graves et al., 2010; Price, 2000; Seghier, 2013). Our study is the first to show a negative ambiguity effect in TPJ. Several studies found positive activation for homophones in left, right or bilateral IPL, SMG or AG (Balthasar, Huber, & Weis, 2011; Chan et al., 2004; Ketteler et al., 2008, 2014; Klepousniotou et al., 2014; Newman & Joanisse, 2011). However, most of these studies did not compare ambiguous to unambiguous words (Klepousniotou et al., 2014; Newman & Joanisse, 2011), or used complex tasks in which multiple meanings of the homonym were presented together (Balthasar et al., 2011; Ketteler et al., 2008, 2014), and in any case did not differentiate between the two phases of processing ambiguous words as done in the current study, so it is not clear how to interpret this increase in activation in TPJ.

The pattern of activation for ambiguous words in the current study, showing reduced activation in TPJ, accompanied by increased activation in frontal regions, is consistent with another fMRI study of ambiguous words showing a dissociation between frontal and posterior parietal regions (Whitney, Grossman, & Kircher, 2009). This dissociation suggests that in reading ambiguous words there is a decrease in reliance on bottom-up automatic processes for mapping orthography to phonology and semantics, and an increase in controlled top-down retrieval and selection processes associated with frontal areas due to the conflicting information (Whitney et al., 2009). This interpretation is consistent with the notion that left IFG is involved in controlled linguistic processes (Bitan, Booth, et al., 2005; Fiebach, Ricker, Friederici, & Jacobs, 2007; Roskies, Fiez, Balota, Raichle, & Petersen, 2001). More specifically, the lower activation in left AG, associated with lexical semantic processes, in heterophones compared to homophones is consistent with the lower activation in bilateral IFG pars orbitalis in the same comparison. The association of AG and orbitalis with semantic processes suggest less involvement of a semantic conflict in heterophones compared to homophones.

An alternative interpretation for the negative ambiguity effect in TPJ is the fact that ambiguous words were one letter shorter on average than unambiguous words (0.6 less consonants, and 0.3 less vowel letters in ambiguous words). However, this interpretation is not consistent with the results of a recent study (Weiss, Katzir, & Bitan, 2015) showing that unpointed Hebrew words with more vowel letters resulted in *less* activation in all parts of left TPJ, and that more consonant letters had no effect on TPJ. Hence, the difference in word length between ambiguous and unambiguous words would predict less (and not more) activation for unambiguous compared to ambiguous words in TPJ, and therefore, it cannot explain the negative ambiguity effects we found in TPJ.

Phase 2: Integration of the Homograph With the Context

Phase 2 begins with the presentation of the target word (the context) and reflects the integration of the ambiguous word with the context, resulting in the final disambiguation process. Our behavioral results show slower responses and more errors for target words related to the subordinate meaning of both heterophones and homophones compared to target words related to the dominant meanings and compared to target words related to unambiguous words. This is consistent with previous studies (Burgess & Simpson, 1988; Peleg & Eviatar, 2008, 2009, 2012), and reflects the need to revisit the selected lexical representation when the subordinate context is presented and select a different meaning that is more appropriate for the context. The ambiguity effect was larger for heterophones compared to homophones, consistent with previous findings (Peleg et al., 2012; Peleg & Eviatar, 2008, 2009, 2012), suggesting that the disengagement from the selected dominant meaning or the selection of the subordinate meaning is more difficult in heterophones.

Our imaging results show a positive ambiguity effect for target words related to the subordinate meaning for heterophones in all left IFG regions and for homophones in bilateral opercularis and bilateral triangularis. We also find a negative ambiguity effect for target words related to the dominant meaning only for heterophones in bilateral IFG (all regions except right Orb) and in left TPJ (SMG and IPL). When taking the difference between dominant and subordinate meanings as a measure for the effect of meaning salience, similar patterns emerged for frontal and posterior regions. Namely, overall effects of meaning salience were larger in the left than in the RH (IFG, IPL) and were larger for heterophones compared to homophones (IFG, IPL and SMG). The difference between heterophones and homophones in the effect of meaning salience is also larger in the LH (IFG and IPL). Finally, the regions showing the strongest effect of meaning salience within IFG were bilateral opercularis and triangularis (>orbitalis), and the regions showing the strongest effect of meaning salience within TPJ are left SMG and bilateral IPL (>AG).

Our result for homophones, showing a greater ambiguity effect for the subordinate meaning in bilateral opercularis and triangularis, are consistent with previous neuroimaging studies showing activation in left and right IFG pars triangularis and opercularis in subordinated compared to dominant meanings of ambiguous words (Bilenko et al., 2009; Mason & Just, 2007; Zempleni et al., 2007). Left IFG was also specifically implicated in the disambiguation phase in studies that attempted to dissociate the two phases

(Acheson & Hagoort, 2013; Peretz & Lavidor, 2013; Rodd et al., 2012). This finding, together with the behavioral evidence for a larger ambiguity effect for the subordinate compared to the dominant meaning, suggests that the presentation of the unexpected subordinate context increases demands on lexical selection processes, required for finding and reactivating the subordinate meaning. This increases the processing load in both hemispheres.

Heterophones show a positive ambiguity effect for the subordinate meaning in left IFG, which is consistent with homophones and with previous studies (see above). However, heterophones also showed a negative ambiguity effect for the dominant meaning in bilateral IFG, left IPL, and left SMG. Although this was unexpected it resulted in overall larger effects of meaning salience in heterophones compared to homophones in these regions, which is consistent with our hypothesis. It is also consistent with our behavioral findings, and those of previous studies, (Peleg et al., 2012; Peleg & Eviatar, 2008, 2009, 2012) showing stronger ambiguity effects for heterophones compared to homophones. These results suggest that when reading heterophones, it is more difficult to disengage from the selected dominant meaning and reactivate the subordinate meaning compared to reading of homophones. This may be due to greater commitment to the selection of the dominant meaning of heterophones compared to homophones in Phase 1. Moreover, the negative ambiguity effect for the dominant meaning of heterophones compared to target words related to unambiguous words may reflect a strong priming (facilitation) effect from the dominant meaning already selected during Phase 1 to the related target word presented in Phase 2. The intensive conflict and selection process for heterophones in Phase 1 may have created stronger activation of the selected representation that facilitates processing of the dominant related target word, even more than the priming effect that occurs in unambiguous words.

The regions showing the largest difference between heterophones and homophones in the effect of meaning salience were bilateral opercularis (within IFG), and bilateral IPL and left SMG (within TPJ), and overall these effects were larger in the left compared to the RH. These regions have been previously associated with phonological segmentation, phonological decoding and with lexical phonology (Bitan et al., 2007; Bitan, Manor, et al., 2005; Hartwigsen et al., 2010; Poldrack et al., 1999; Price, 2012; Vigneau et al., 2006; Wheat et al., 2010). These findings are consistent with our predictions and with the idea that the ambiguity resolution in heterophones involves primarily phonological processes, as indicated in the discussion on Phase 1, and that mapping of orthography to phonology is more left lateralized than mapping from orthography to meaning (Peleg & Eviatar, 2008, 2009, 2012). Our findings are also consistent with the notion that a ventral more bilateral route is related to semantic access, while a dorsal more left lateralized route is related to phonological access and planning (Hickok & Poeppel, 2007).

The limitation of the current study is its low temporal resolution, typical of fMRI studies. Moreover, to separate between the two phases of ambiguity processing the interval between the ambiguous word and the context was 2.7 s. Although this interval reflects an ecologically valid situation, in which the context could appear a few seconds after the ambiguous word in a sentence, it may not allow us to distinguish among time sensitive processes. This may be especially critical given the sensitivity of the hemispheric lateralization to timing, as evident by the differential findings for stimulus onset asynchrony (SOAs) of 100, 250 and 1000ms in previous DVF experiments (Peleg & Eviatar, 2008, 2009, 2012). At the time scale of 2.7 s interval between the two phases, tested in the current study, information could transfer between hemispheres, and this could mask larger hemispheric differences than those reported here.

Conclusions

Our results show that heterophonic homographs (which are phonologically ambiguous) are processed differently than homophonic homographs (which are phonologically unambiguous). Specifically, heterophones show greater activation compared to homophones in regions associated with phonological processing, and less activation then homophones in regions associated with semantic processing, suggesting that phonological disambiguation occurs prior to the completion of the semantic disambiguation process. Thus, although lexical ambiguity resolution is typically treated as a unitary phenomenon, the results of the present study demonstrate that the phonological status of the homograph determines which mechanisms are recruited and their laterality (for similar results with other types of homographs, see Lee & Federmeier, 2006, 2009, 2012). In particular, we show that when homographs are presented without a biasing context, the conflict and selection process in heterophones tend to occur at the phonological level, thus relying more on the LH. In contrast, the lexical selection in homophones occurs at the lexical semantic level, and is bilateral. Furthermore, the presemantic phonological disambiguation process, in the case of heterophones, results in a stronger commitment to the dominant representation, which is then reflected in greater difficulty in retrieval of the subordinate meaning when the subordinate context is presented.

Such results indicate that phonology may play a much more important role in the extraction of meaning from print than dual route models (e.g., Coltheart et al., 2001) have assumed for familiar words. Thus, at least in the case of Hebrew homographs, our results support the idea that the processing of a printed word is influenced by information concerning its pronunciation (Ferrand & Grainger, 2003; Frost, 1998; Seidenberg & McClelland, 1989). It is important to note that although previous fMRI studies have reported phonological effects in visual word recognition (e.g., Carreiras et al., 2014; Jobard et al., 2003; Pugh et al., 1996; Taylor et al., 2013) these findings cannot distinguish between dual route models and “triangle” connectionist models, because both predict phonological effects when nonwords and/or phonological tasks are involved. The novelty of the current study is showing this prominent role of phonology even in a task that emphasizes semantic rather than phonological processes, and even when the printed word is highly familiar. Thus, consistent with connectionist “triangle” models (Ferrand & Grainger, 2003; Seidenberg & McClelland, 1989), we show that visual word recognition always involves a dynamic interplay between orthographic, phonological and semantic processes.

Our study is the first to report a decrease in activation in ambiguous compared to unambiguous words in temporo-parietal regions associated with mapping of orthography to phonology and semantics, in addition to the increase in activation in frontal regions associated with controlled selection processes. If this is a true difference between the results of the current and previous studies, it may reflect a unique property of the Hebrew orthography, which is fraught with homographs and specifically with heterophones due to the sparse representation of vowels. Cross-linguistic differences in orthographic transparency may shape the readers' neural reading mechanisms (Das, Padakannaya, Pugh, & Singh, 2011; Meschyan & Hernandez, 2006; Paulesu et al., 2000). Hebrew readers may be more inclined to retract from the standard bottom-up pathways of mapping orthography to higher level representations when they encounter such a word, and shift to a top-down approach (Shimron, 2006) resulting in a negative ambiguity effect in temporo-parietal regions. The abundance of heterophones could also contribute to enhanced selection of the dominant meaning or to the reliance on phonological regions for resolving the ambiguity. Nevertheless, while the specific level of phonological activation may differ across orthographies with different proportions of homographs, the general principles identified in the current study, namely, that phonological ambiguity can modulate the lateralization and processing of semantic ambiguity, can be generalized to other orthographies.

To summarize, this is the first fMRI study that compares the disambiguation process of homophones and heterophones. Moreover, this is the first study that dissociates lexical and contextual effects in ambiguity resolution. This design enabled us to examine phonological, lexical, and contextual effects in semantic ambiguity resolution. Thus, we were able to address two important issues in language processing: (a) the role of phonology and its interactions with semantic processing in reading, and (b) the role of the RH in processing semantic ambiguity. Taken together, our findings are consistent with (a) the prominent role of phonology in visual word recognition, even in tasks that emphasize semantic rather than phonological processes; (b) with behavioral findings showing that the LH is more influenced by the phonological aspects of written words than the RH (e.g., 2005; Lavidor & Ellis, 2003; Peleg et al., 2012; Peleg & Eviatar, 2009; Smolka & Eviatar, 2006; Zaidel & Peters, 1981); and (c) with the notion of greater left lateralization of phonological compared to semantic processes (Hickok & Poeppel, 2004; Spironelli & Angrilli, 2006; Vigneau et al., 2011) found in other tasks and languages. Furthermore, despite the critical role assumed for the RH in activating and maintaining the subordinate meaning, and integrating the ambiguous word with the context (Copland, Chenery, & Murdoch, 2002; Faust & Chiarello, 1998; M. Faust & Gernsbacher, 1996; Jung-Beeman, 2005), the current evidence suggests that most of these processes are strongly left lateralized.

References

Acheson, D. J., & Hagoort, P. (2013). Stimulating the brain's language network: Syntactic ambiguity resolution after TMS to the inferior frontal gyrus and middle temporal gyrus. *Journal of Cognitive Neuroscience, 25,* 1664–1677. http://dx.doi.org/10.1162/jocn_a_00430

Balthasar, A. J. R., Huber, W., & Weis, S. (2011). A supramodal brain substrate of word form processing—an fMRI study on homonym finding with auditory and visual input. *Brain Research, 1410,* 48–63. http://dx.doi.org/10.1016/j.brainres.2011.06.054

Banich, M. T. (2003). Interaction between the hemispheres and its implications for the processing capacity of the brain. In R. Davidson & K. Hughdahl (Eds.), *Brain asymmetry* (2nd ed., pp. 261–302). Cambridge, MA: MIT press.

Bedny, M., Hulbert, J. C., & Thompson-Schill, S. L. (2007). Understanding words in context: The role of Broca's area in word comprehension. *Brain Research, 1146,* 101–114. http://dx.doi.org/10.1016/j.brainres.2006.10.012

Bedny, M., McGill, M., & Thompson-Schill, S. L. (2008). Semantic adaptation and competition during word comprehension. *Cerebral Cortex, 18,* 2574–2585. http://dx.doi.org/10.1093/cercor/bhn018

Bennett, I. J., Rivera, H. G., & Rypma, B. (2013). Isolating age-group differences in working memory load-related neural activity: Assessing the contribution of working memory capacity using a partial-trial fMRI method. *NeuroImage, 72,* 20–32. http://dx.doi.org/10.1016/j.neuroimage.2013.01.030

Berardi, N., & Fiorentini, A. (1997). Interhemispheric transfer of spatial and temporal frequency information. In S. Christman (Ed.), *Cerebral asymmetries in sensory and perceptual processing* (pp. 55–79). New York, NY: Elsevier Science.

Bilenko, N. Y., Grindrod, C. M., Myers, E. B., & Blumstein, S. E. (2009). Neural correlates of semantic competition during processing of ambiguous words. *Journal of Cognitive Neuroscience, 21,* 960–975. http://dx.doi.org/10.1162/jocn.2009.21073

Binder, J. R., McKiernan, K. A., Parsons, M. E., Westbury, C. F., Possing, E. T., Kaufman, J. N., & Buchanan, L. (2003). Neural correlates of lexical access during visual word recognition. *Journal of Cognitive Neuroscience, 15,* 372–393. http://dx.doi.org/10.1162/089892903321593108

Bitan, T., Booth, J. R., Choy, J., Burman, D. D., Gitelman, D. R., & Mesulam, M.-M. (2005). Shifts of effective connectivity within a language network during rhyming and spelling. *The Journal of Neuroscience, 25,* 5397–5403. http://dx.doi.org/10.1523/JNEUROSCI.0864-05.2005

Bitan, T., Burman, D. D., Chou, T. L., Lu, D., Cone, N. E., Cao, F., . . . Booth, J. R. (2007). The interaction between orthographic and phonological information in children: An fMRI study. *Human Brain Mapping, 28,* 880–891. http://dx.doi.org/10.1002/hbm.20313

Bitan, T., Lifshitz, A., Breznitz, Z., & Booth, J. R. (2010). Bidirectional connectivity between hemispheres occurs at multiple levels in language processing but depends on sex. *The Journal of Neuroscience, 30,* 11576–11585. http://dx.doi.org/10.1523/JNEUROSCI.1245-10.2010

Bitan, T., Manor, D., Morocz, I. A., & Karni, A. (2005). Effects of alphabeticality, practice and type of instruction on reading an artificial script: An fMRI study. *Cognitive Brain Research, 25,* 90–106. http://dx.doi.org/10.1016/j.cogbrainres.2005.04.014

Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002, June). *Region of interest analysis using an SPM toolbox*. Paper presented at the Human Brain Mapping, Sendai, Japan.

Burgess, C., & Simpson, G. B. (1988). Cerebral hemispheric mechanisms in the retrieval of ambiguous word meanings. *Brain and Language, 33,* 86–103. http://dx.doi.org/10.1016/0093-934X(88)90056-9

Carreiras, M., Armstrong, B. C., Perea, M., & Frost, R. (2014). The what, when, where, and how of visual word recognition. *Trends in Cognitive Sciences, 18,* 90–98. http://dx.doi.org/10.1016/j.tics.2013.11.005

Chan, A. H. D., Liu, H. L., Yip, V., Fox, P. T., Gao, J. H., & Tan, L. H. (2004). Neural systems for word meaning modulated by semantic ambiguity. *NeuroImage, 22,* 1128–1133. http://dx.doi.org/10.1016/j.neuroimage.2004.02.034

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review, 108,* 204–256. http://dx.doi.org/10.1037/0033-295X.108.1.204

Copland, D. A., Chenery, H. J., & Murdoch, B. E. (2002). Hemispheric contributions to lexical ambiguity resolution: Evidence from individuals with complex language impairment following left-hemisphere lesions. *Brain and Language, 81,* 131–143. http://dx.doi.org/10.1006/brln.2001.2512

Coulson, S., Federmeier, K., Van Petten, C., & Kutas, M. (2005). Right hemisphere sensitivity to word and sentence level context: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Earning, Memory, and Cognition, 31,* 129–147.

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping, 8,* 109–114.

Das, T., Padakannaya, P., Pugh, K. R., & Singh, N. C. (2011). Neuroimaging reveals dual routes to reading in simultaneous proficient readers of two orthographies. *NeuroImage, 54,* 1476–1487. http://dx.doi.org/10.1016/j.neuroimage.2010.09.022

Dehaene, S. (2009). *Reading in the brain*. London, UK: Viking Penguin.

Démonet, J. F., Thierry, G., & Cardebat, D. (2005). Renewal of the neurophysiology of language: Functional neuroimaging. *Physiological Reviews, 85,* 49–95. http://dx.doi.org/10.1152/physrev.00049.2003

Duffy, S. A., Morris, R. K., & Rayner, K. (1988). Lexical ambiguity and fixation times in reading. *Journal of Memory and Language, 27,* 429–446. http://dx.doi.org/10.1016/0749-596X(88)90066-6

Faust, M., & Chiarello, C. (1998). Sentence context and lexical ambiguity resolution by the two hemispheres. *Neuropsychologia, 36,* 827–835. http://dx.doi.org/10.1016/s0028-3932(98)00042-6

Faust, M. E., & Gernsbacher, M. A. (1996). Cerebral mechanisms for suppression of inappropriate information during sentence comprehension. *Brain and Language, 53,* 234–259. http://dx.doi.org/10.1006/brln.1996.0046

Federmeier, K. D., & Kutas, M. (1999). Right words and left words: Electrophysiological evidence for hemispheric differences in meaning processing. *Cognitive Brain Research, 8,* 373–392. http://dx.doi.org/10.1016/S0926-6410(99)00036-1

Ferrand, L., & Grainger, J. (2003). Homophone interference effects in visual word recognition. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology, 56,* 403–419. http://dx.doi.org/10.1080/02724980244000422

Fiebach, C. J., Ricker, B., Friederici, A. D., & Jacobs, A. M. (2007). Inhibition and facilitation in visual word recognition: Prefrontal contribution to the orthographic neighborhood size effect. *NeuroImage, 36,* 901–911. http://dx.doi.org/10.1016/j.neuroimage.2007.04.004

Frost, R. (1998). Toward a strong phonological theory of visual word recognition: True issues and false trails. *Psychological Bulletin, 123,* 71–99. http://dx.doi.org/10.1037/0033-2909.123.1.71

Gennari, S. P., MacDonald, M. C., Postle, B. R., & Seidenberg, M. S. (2007). Context-dependent interpretation of words: Evidence for interactive neural processes. *NeuroImage, 35,* 1278–1286. http://dx.doi.org/10.1016/j.neuroimage.2007.01.015

Giora, R. (2003). *On our mind: Salience, context, and figurative language*. New York, NY: Oxford University Press. http://dx.doi.org/10.1093/acprof:oso/9780195136166.001.0001

Gold, B. T., Balota, D. A., Kirchhoff, B. A., & Buckner, R. L. (2004). Common and dissociable activation patterns associated with controlled semantic and phonological processing: Evidence from fMRI adaptation. *Cerebral Cortex, 15,* 1438–1450. http://dx.doi.org/10.1093/cercor/bhi024

Graves, W. W., Desai, R., Humphries, C., Seidenberg, M. S., & Binder, J. R. (2010). Neural systems for reading aloud: A multiparametric approach. *Cerebral Cortex, 20,* 1799–1815. http://dx.doi.org/10.1093/cercor/bhp245

Halderman, L. K., & Chiarello, C. (2005). Cerebral asymmetries in early orthographic and phonological reading processes: Evidence from backward masking. *Brain and Language, 95,* 342–352. http://dx.doi.org/10.1016/j.bandl.2005.02.005

Harm, M. W., & Seidenberg, M. S. (1999). Phonology, reading acquisition, and dyslexia: Insights from connectionist models. *Psychological Review, 106,* 491–528. http://dx.doi.org/10.1037/0033-295X.106.3.491

Harm, M. W., & Seidenberg, M. S. (2004). Computing the meanings of words in reading: Cooperative division of labor between visual and phonological processes. *Psychological Review, 111,* 662–720. http://dx.doi.org/10.1037/0033-295X.111.3.662

Hartwigsen, G., Baumgaertner, A., Price, C. J., Koehnke, M., Ulmer, S., & Siebner, H. R. (2010). Phonological decisions require both the left and right supramarginal gyri. *Proceedings of the National Academy of Sciences of the United States of America, 107,* 16494–16499. http://dx.doi.org/10.1073/pnas.1008121107

Henson, R., Buchel, C., Josephs, O., & Friston, K. (1999). The slice-timing problem in event-related fMRI. *Neuroimage, 9,* S125.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition, 92,* 67–99. http://dx.doi.org/10.1016/j.cognition.2003.10.011

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8,* 393–402. http://dx.doi.org/10.1038/nrn2113

Ihara, A., Hayakawa, T., Wei, Q., Munetsuna, S., & Fujimaki, N. (2007). Lexical access and selection of contextually appropriate meaning for ambiguous words. *NeuroImage, 38,* 576–588. http://dx.doi.org/10.1016/j.neuroimage.2007.07.047

Ihara, A. S., Mimura, T., Soshi, T., Yorifuji, S., Hirata, M., Goto, T., . . . Fujimaki, N. (2015). Facilitated lexical ambiguity processing by transcranial direct current stimulation over the left inferior frontal cortex. *Journal of Cognitive Neuroscience, 27,* 26–34. http://dx.doi.org/10.1162/jocn_a_00703

January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of stroop and syntactic ambiguity resolution in Broca's area: Implications for the neural basis of sentence processing. *Journal of Cognitive Neuroscience, 21,* 2434–2444. http://dx.doi.org/10.1162/jocn.2008.21179

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A metanalysis of 35 neuroimaging studies. *NeuroImage, 20,* 693–712. http://dx.doi.org/10.1016/S1053-8119(03)00343-4

Jung-Beeman, M. (2005). Bilateral brain processes for comprehending natural language. *Trends in Cognitive Sciences, 9,* 512–518. http://dx.doi.org/10.1016/j.tics.2005.09.009

Ketteler, D., Kastrau, F., Vohn, R., & Huber, W. (2008). The subcortical role of language processing. High level linguistic features such as ambiguity-resolution and the human brain; an fMRI study. *NeuroImage, 39,* 2002–2009. http://dx.doi.org/10.1016/j.neuroimage.2007.10.023

Ketteler, S., Ketteler, D., Vohn, R., Kastrau, F., Schulz, J. B., Reetz, K., & Huber, W. (2014). The processing of lexical ambiguity in healthy ageing and Parkinson's disease: Role of cortico-subcortical networks. *Brain Research, 1581,* 51–63. http://dx.doi.org/10.1016/j.brainres.2014.06.030

Klepousniotou, E., Gracco, V. L., & Pike, G. B. (2014). Pathways to lexical ambiguity: fMRI evidence for bilateral fronto-parietal involvement in language processing. *Brain and Language, 131,* 56–64. http://dx.doi.org/10.1016/j.bandl.2013.06.002

Lavidor, M., & Ellis, A. W. (2003). Orthographic and phonological priming in the two cerebral hemispheres. *Laterality: Asymmetries of Body, Brain and Cognition, 8,* 201–223. http://dx.doi.org/10.1080/13576500143000203

Lee, C. L., & Federmeier, K. D. (2006). To mind the mind: An event-related potential study of word class and semantic ambiguity. *Brain Research, 1081,* 191–202. http://dx.doi.org/10.1016/j.brainres.2006.01.058

Lee, C. L., & Federmeier, K. D. (2009). Wave-ering: An ERP study of syntactic and semantic context effects on ambiguity resolution for noun/verb homographs. *Journal of Memory and Language, 61,* 538–555. http://dx.doi.org/10.1016/j.jml.2009.08.003

Lee, C. L., & Federmeier, K. D. (2012). Ambiguity's aftermath: How age differences in resolving lexical ambiguity affect subsequent comprehension. *Neuropsychologia, 50,* 869–879. http://dx.doi.org/10.1016/j.neuropsychologia.2012.01.027

Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage, 19,* 1233–1239. http://dx.doi.org/10.1016/S1053-8119(03)00169-1

Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 18,* 492–508. http://dx.doi.org/10.1037/0278-7393.18.3.492

Marsolek, C. J., Schacter, D. L., & Nicholas, C. D. (1996). Form-specific visual priming for new associations in the right cerebral hemisphere. *Memory & Cognition, 24,* 539–556. http://dx.doi.org/10.3758/BF03201082

Mason, R. A., & Just, M. A. (2007). Lexical ambiguity in sentence comprehension. *Brain Research, 1146,* 115–127. http://dx.doi.org/10.1016/j.brainres.2007.02.076

Meltzer, J. A., McArdle, J. J., Schafer, R. J., & Braun, A. R. (2010). Neural aspects of sentence comprehension: Syntactic complexity, reversibility, and reanalysis. *Cerebral Cortex, 20,* 1853–1864. http://dx.doi.org/10.1093/cercor/bhp249

Meschyan, G., & Hernandez, A. E. (2006). Impact of language proficiency and orthographic transparency on bilingual word reading: An fMRI investigation. *NeuroImage, 29,* 1135–1140. http://dx.doi.org/10.1016/j.neuroimage.2005.08.055

Moss, H. E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., & Tyler, L. K. (2005). Selecting among competing alternatives: Selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex, 15,* 1723–1735. http://dx.doi.org/10.1093/cercor/bhi049

Newman, R. L., & Joanisse, M. F. (2011). Modulation of brain regions involved in word recognition by homophonous stimuli: An fMRI study. *Brain Research, 1367,* 250–264. http://dx.doi.org/10.1016/j.brainres.2010.09.089

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective & Behavioral Neuroscience, 5,* 263–281. http://dx.doi.org/10.3758/CABN.5.3.263

Ollinger, J. M., Corbetta, M., & Shulman, G. L. (2001). Separating processes within a trial in event-related functional MRI II. Analysis. *NeuroImage, 13,* 218–229. http://dx.doi.org/10.1006/nimg.2000.0711

Ollinger, J. M., Shulman, G. L., & Corbetta, M. (2001). Separating processes within a trial in event-related functional MRI I. The Method. *NeuroImage, 13,* 210–217. http://dx.doi.org/10.1006/nimg.2000.0710

Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S. F., . . . Frith, U. (2000). A cultural effect on brain function. *Nature Neuroscience, 3,* 91–96. http://dx.doi.org/10.1038/71163

Peleg, O., & Eviatar, Z. (2008). Hemispheric sensitivities to lexical and contextual information: Evidence from lexical ambiguity resolution. *Brain and Language, 105,* 71–82. http://dx.doi.org/10.1016/j.bandl.2007.09.004

Peleg, O., & Eviatar, Z. (2009). Semantic asymmetries are modulated by phonological asymmetries: Evidence from the disambiguation of homophonic versus heterophonic homographs. *Brain and Cognition, 70,* 154–162. http://dx.doi.org/10.1016/j.bandc.2009.01.007

Peleg, O., & Eviatar, Z. (2012). Understanding written words: Phonological, lexical and contextual effects in the two cerebral hemispheres. In M. Faust (Ed.), *Neuropsychology of language: Advances in the neural substrates of language* (pp. 59–76). New York, NY: Wiley. http://dx.doi.org/10.1002/9781118432501.ch4

Peleg, O., Giora, R., & Fein, O. (2001). Salience and context effects: Two are better than one. *Metaphor and Symbol, 16,* 173–192. http://dx.doi.org/10.1080/10926488.2001.9678894

Peleg, O., Giora, R., & Fein, O. (2004). Contextual strength: The whens and hows of context effects. In I. N. D. Sperber (Ed.), *Experimental pragmatics* (pp. 172–186). Basingstoke, UK: Pagrave. http://dx.doi.org/10.1057/9780230524125_8

Peleg, O., Markus, A., & Eviatar, Z. (2012). Hemispheric asymmetries in meaning selection: Evidence from the disambiguation of homophonic vs. heterophonic homographs. *Brain and Cognition, 80,* 328–337. http://dx.doi.org/10.1016/j.bandc.2012.08.005

Peretz, Y., & Lavidor, M. (2013). Enhancing lexical ambiguity resolution by brain polarization of the right posterior superior temporal sulcus. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior, 49,* 1056–1062. http://dx.doi.org/10.1016/j.cortex.2012.03.015

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage, 10,* 15–35. http://dx.doi.org/10.1006/nimg.1999.0441

Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2006). Neural systems for orienting attention to the location of threat signals: An event-related fMRI study. *NeuroImage, 31,* 920–933. http://dx.doi.org/10.1016/j.neuroimage.2005.12.034

Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy, 197,* 335–359. http://dx.doi.org/10.1046/j.1469-7580.2000.19730335.x

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62,* 816–847. http://dx.doi.org/10.1016/j.neuroimage.2012.04.062

Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., . . . Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain: A Journal of Neurology, 119,* 1221–1238. http://dx.doi.org/10.1093/brain/119.4.1221

Rayner, K., Pollmann, S., Ashby, J., & Clifton, C. (2012). *Psychology of reading*. New York, NY: Psychology Press.

Ripamonti, E., Traficante, D., Crippa, F., & Luzzattii, C. (2014). Word and pseudoword superiority effects in a shallow orthography language: The role of hemispheric lateralization. *Perceptual and Motor Skills, 118,* 411–428. http://dx.doi.org/10.2466/22.19.PMS.118k20w6

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex, 15,* 1261–1269. http://dx.doi.org/10.1093/cercor/bhi009

Rodd, J. M., Johnsrude, I. S., & Davis, M. H. (2012). Dissociating frontotemporal contributions to semantic ambiguity resolution in spoken sentences. *Cerebral Cortex, 22,* 1761–1773. http://dx.doi.org/10.1093/cercor/bhr252

Rodd, J. M., Vitello, S., Woollams, A. M., & Adank, P. (2015). Localising semantic and syntactic processing in spoken and written language comprehension: An activation likelihood estimation meta-analysis. *Brain and Language, 141,* 89–102. http://dx.doi.org/10.1016/j.bandl.2014.11.012

Roskies, A. L., Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (2001). Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *Journal of Cognitive Neuroscience, 13,* 829–843. http://dx.doi.org/10.1162/08989290152541485

Ruge, H., Goschke, T., & Braver, T. S. (2009). Separating event-related BOLD components within trials: The partial-trial design revisited. *NeuroImage, 47,* 501–513. http://dx.doi.org/10.1016/j.neuroimage.2009.04.075

Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *The Neuroscientist, 19,* 43–61. http://dx.doi.org/10.1177/1073858412440596

Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review, 96,* 523–568. http://dx.doi.org/10.1037/0033-295X.96.4.523

Shimron, J. (2006). *Reading Hebrew: The language and the psychology of reading it*. Mahwah, NJ: Erlbaum.

Smolka, E., & Eviatar, Z. (2006). Phonological and orthographic visual word recognition in the two cerebral hemispheres: Evidence from Hebrew. *Cognitive Neuropsychology, 23,* 972–989. http://dx.doi.org/10.1080/02643290600654855

Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J. A., Petersson, K. M., & Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: An fMRI study using word-category ambiguity. *Cerebral Cortex, 19,* 1493–1503. http://dx.doi.org/10.1093/cercor/bhn187

Spironelli, C., & Angrilli, A. (2006). Language lateralization in phonological, semantic and orthographic tasks: A slow evoked potential study. *Behavioural Brain Research, 175,* 296–304. http://dx.doi.org/10.1016/j.bbr.2006.08.038

Taylor, J. S. H., Rastle, K., & Davis, M. H. (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychological Bulletin, 139,* 766–791. http://dx.doi.org/10.1037/a0030266

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences of the United States of America, 94,* 14792–14797. http://dx.doi.org/10.1073/pnas.94.26.14792

Titone, D. (1998). Hemispheric differences in context sensitivity during lexical ambiguity resolution. *Brain and Language, 65,* 361–394. http://dx.doi.org/10.1006/brln.1998.1998

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., . . . Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage, 30,* 1414–1432. http://dx.doi.org/10.1016/j.neuroimage.2005.11.002

Vigneau, M., Beaucousin, V., Hervé, P. Y., Jobard, G., Petit, L., Crivello, F., . . . Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *NeuroImage, 54,* 577–593. http://dx.doi.org/10.1016/j.neuroimage.2010.07.036

Vitello, S., Warren, J. E., Devlin, J. T., & Rodd, J. M. (2014). Roles of frontal and temporal regions in reinterpreting semantically ambiguous sentences. *Frontiers in Human Neuroscience, 8,* 530. http://dx.doi.org/10.3389/fnhum.2014.00530

Waldie, K. E., Haigh, C. E., Badzakova-Trajkov, G., Buckley, J., & Kirk, I. J. (2013). Reading the wrong way with the right hemisphere. *Brain Sciences, 3,* 1060–1075. http://dx.doi.org/10.3390/brainsci3031060

Weiss, Y., Katzir, T., & Bitan, T. (2015). Many ways to read your vowels—neural processing of diacritics and vowel letters in Hebrew. *NeuroImage, 121,* 10–19. http://dx.doi.org/10.1016/j.neuroimage.2015.07.029

Wheat, K. L., Cornelissen, P. L., Frost, S. J., & Hansen, P. C. (2010). During visual word recognition, phonology is accessed within 100 ms and may be mediated by a speech production code: Evidence from magnetoencephalography. *The Journal of Neuroscience, 30,* 5229–5233. http://dx.doi.org/10.1523/JNEUROSCI.4448-09.2010

Whitney, C., Grossman, M., & Kircher, T. T. J. (2009). The influence of multiple primes on bottom-up and top-down regulation during meaning retrieval: Evidence for 2 distinct neural networks. *Cerebral Cortex, 19,* 2548–2560. http://dx.doi.org/10.1093/cercor/bhp007

Woldorff, M. G., Hazlett, C. J., Fichtenholtz, H. M., Weissman, D. H., Dale, A. M., & Song, A. W. (2004). Functional parcellation of attentional control regions of the brain. *Journal of Cognitive Neuroscience, 16,* 149–165. http://dx.doi.org/10.1162/089892904322755638

Zaidel, E. (1998). Language in the right hemisphere following callosal disconnection. In B. Stemmer & H. Whitaker (Eds.), *Handbook of neurolinguistics* (pp. 369–383). San Diego, CA: Academic Press. http://dx.doi.org/10.1016/B978-012666055-5/50029-0

Zaidel, E., & Peters, A. M. (1981). Phonological encoding and ideographic reading by the disconnected right hemisphere: Two case studies. *Brain and Language, 14,* 205–234. http://dx.doi.org/10.1016/0093-934X(81)90077-8

Zempleni, M. Z., Renken, R., Hoeks, J. C. J., Hoogduin, J. M., & Stowe, L. A. (2007). Semantic ambiguity processing in sentence context: Evidence from event-related fMRI. *NeuroImage, 34,* 1270–1279. http://dx.doi.org/10.1016/j.neuroimage.2006.09.048

Ziegler, J. C., & Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: A psycholinguistic grain size theory. *Psychological Bulletin, 131,* 3–29. http://dx.doi.org/10.1037/0033-2909.131.1.3

Received June 4, 2016
Revision received January 4, 2017
Accepted January 5, 2017 ■