Article:

MacGregor, LJ, Bouwsema, J and Klepousniotou, E orcid.org/0000-0002-2318-0951 (2015) Sustained meaning activation for polysemous but not homonymous words: Evidence from EEG. Neuropsychologia, 68. pp. 126-138. ISSN 0028-3932

https://doi.org/10.1016/j.neuropsychologia.2015.01.008

Sustained meaning activation for polysemous but not homonymous words: Evidence from EEG

Lucy J MacGregor[1], Jennifer Bouwsema[2], Ekaterini Klepousniotou[3]

[1] MRC Cognition and Brain Sciences Unit, Cambridge

[2] Psychology, University of Stirling

[3] Institute of Psychological Sciences, University of Leeds

Corresponding author:

Dr. Ekaterini Klepousniotou

Institute of Psychological Sciences

University of Leeds

Leeds, LS2 9JT

UK

Tel.: +44 113 343 5716

Fax: +44 113 343 5749

Email: e.klepousniotou@leeds.ac.uk

Abstract

Theoretical linguistic accounts of lexical ambiguity distinguish between homonymy, where words that share a lexical form have unrelated meanings, and polysemy, where the meanings are related. The present study explored the psychological reality of this theoretical assumption by asking whether there is evidence that homonyms and polysemes are represented and processed differently in the brain. We investigated the time-course of meaning activation of different types of ambiguous words using EEG. Homonyms and polysemes were each further subdivided into two: unbalanced homonyms (e.g., “coach”) and balanced homonyms (e.g., “match”); metaphorical polysemes (e.g., “mouth”) and metonymic polysemes (e.g., “rabbit”). These four types of ambiguous words were presented as primes in a visual single-word priming delayed lexical decision task employing a long ISI (750 ms). Targets were related to one of the meanings of the primes, or were unrelated. ERPs formed relative to the target onset indicated that the theoretical distinction between homonymy and polysemy was reflected in the N400 brain response. For targets following homonymous primes (both unbalanced and balanced), no effects survived at this long ISI indicating that both meanings of the prime had already decayed. On the other hand, for polysemous primes (both metaphorical and metonymic), activation was observed for both dominant and subordinate senses. The observed processing differences between homonymy and polysemy provide evidence in support of differential neuro-cognitive representations for the two types of ambiguity. We argue that the polysemous senses act collaboratively to strengthen the representation, facilitating maintenance, while the competitive nature of homonymous meanings leads to decay.

Key words: ERP, N400, Lexical ambiguity, Semantic priming, Homonymy, Polysemy

Highlights

ERP (N400) investigation of meaning activation of ambiguous words at a long ISI.

Evidence for differential neuro-cognitive representations for homonymy and polysemy.

Sustained meaning activation for polysemy but not homonymy.

Polysemous senses act collaboratively to strengthen their core representation.

The competitive nature of homonymous meanings leads to decay.

1. Introduction

Lexical ambiguity, where words share phonology and orthography but refer to more than one concept, is very prevalent in language. Thus, comprehension of ambiguous words is crucial for interpreting the intended message of written or spoken language. Given the ubiquity of ambiguity in language, neuro-cognitive models of word recognition and of language comprehension more generally, must explain how ambiguous words are represented and processed in the brain. The present study explores this issue using EEG methodology and visually presented ambiguous words. We focus in particular on the time-course of activation of ambiguous word meanings, and on what the processing differences between theoretically-proposed types of ambiguity tell us about their representations in the brain.

Ambiguous words do not form a homogeneous category. Theoretical linguistic accounts of lexical ambiguity distinguish between different types of ambiguity with the main distinction being between homonymy and polysemy. Homonymy refers to words where a single lexical form has multiple semantically-unrelated distinct meanings. For example, “coach” means a vehicle used for transport and an individual who trains a sports team. The different meanings of a homonym share a common lexical form by historical accident and accordingly lexicographers list different meanings of homonyms as separate entries in dictionaries. Importantly, psychological data is consistent with the linguistic approach to homonymy and it is widely accepted that the different meanings have distinct lexical representations in the brain (Beretta, Fiorentino, & Poeppel, 2005; Pylkkänen, Llinás, & Murphy, 2006). By contrast, the nature of polysemous representations is far more controversial and less well understood. Polysemy refers to words where a single lexical form has multiple meanings that share a semantic relationship. For example “paper” means a type of material and also the content of a publication such as a newspaper, which is (at least traditionally) printed on paper. Lexicographers list polysemous meanings under the same lexical entry in a dictionary, typically using shared etymology as the important criterion in addition to shared semantics. From a psychological perspective, it is unclear how the different meanings – or senses as they are more often referred – are represented in the brain. Do polysemous senses, like homonymous meanings, have distinct lexical representations in the brain or do they share a single common representation?

The nature of polysemy representation is further complicated because polysemy does not refer to a homogeneous category and there is a broad variety of ways in which polysemous senses are related. Most notably, and again within a theoretical linguistics framework, a distinction can be made between metaphorical polysemy and metonymic polysemy (Apresjan, 1974). Metaphorically polysemous words (also referred to as metaphor) have a primary or literal meaning and a secondary figurative meaning – although with continued use over time the secondary meaning may be perceived as literal. For example, the primary meaning of “mouth” is the opening in the face and the secondary meaning refers more generally to an entrance or opening, for example of a cave. Metaphor links two distinct concepts through analogy (e.g., “mouth”, part of human body and part of a cave). The analogical relation may not always be very salient (Apresjan, 1974) and, moreover, it is irregular and takes many different forms. By contrast with metaphors, both primary and secondary meanings of metonymically polysemous words are literal. Furthermore, the semantic connection between the different meanings is usually transparent and often follows one of a number of systematic patterns (Lehrer, 1990). For example, a word referring to an animal (e.g. “rabbit”, “fish”) often also refers to the meat of that animal, and a word referring to a physical object (e.g. “book”, “DVD”) often also refers to the contents of that object (Pustejovsky, 1995). It has been argued that such linguistic rules make it possible that there is a single basic or core lexical sense from which others are derived online during comprehension (Nunberg, 1979). However, the core meaning proposal is not without problems. Polysemous senses are not always predictable and in some cases, the different senses of polysemes are semantically quite different even if the relation between the two can be easily understood (e.g., “paper” referring to wrapping paper and to the editors at a newspaper, Klein & Murphy, 2001). It has also been argued that for most polysemous words it is difficult to find a single basic sense from which the others can be derived (Zgusta, 1971). Without the possibility of deriving meaning by a linguistic rule, it is argued the senses must be explicitly represented (Cruse, 1986; Lehrer, 1990). Here we investigate the evidence for distinct versus overlapping representations of the senses of metaphors and metonyms as well as homonyms. Before turning to our experiment, we discuss the existing experimental evidence.

1.1. Inconsistent behavioural evidence for representational and processing differences between homonymous and polysemous words

A number of experimental psycholinguistic studies have investigated whether the aforementioned linguistic claims and assumptions have a psychological reality, with mixed results. Several studies that directly compared the processing of homonyms and polysemes concluded that representational differences do exist between the two types. For example, during reading, polysemes were associated with shorter fixation times than homonymous words (Frazier & Rayner, 1990). This finding was used to argue that different senses of polysemous words are complementary, not incompatible, and thus selection of a specific sense is not required immediately for processing to continue. In contrast, the distinct meanings of homonyms compete for activation or selection, which delays processing. Further evidence for a distinction between homonyms and polysemes comes from lexical decision tasks in which reaction times were faster to polysemous words than to unambiguous words, but slower to homonymous words (Beretta et al., 2005; Klepousniotou & Baum, 2007; Rodd, Gaskell, & Marslen-Wilson, 2002). The processing disadvantage observed for homonymous words is also well explained by an account of word recognition in which the different meanings of the homonym compete for activation or selection, whereas the facilitation observed for processing polysemous senses reflects either co-activation of multiple senses which perhaps form a rich semantic representation, or activation of an underspecified representation where selection of a specific sense is not required.

Another way to assess the way in which different types of ambiguous words are processed and represented is to probe the activation of the various meanings of ambiguous words by measuring semantic priming effects. For example, in a lexical decision task, where faster responses to targets are observed when the target is preceded by a related compared to an unrelated prime (e.g., a word, a sentence or a picture), the response facilitation reflects the fact that the prime leads to pre-activation of the target meaning or results in easier post-lexical integration. In the case of ambiguous primes, the method can be used to see whether a particular meaning of a given word primes a subsequent target, and hence to draw conclusions about whether that meaning was activated. Likewise, a sentence context can be used to prime a particular meaning of a subsequently presented ambiguous target and compared for ambiguous primes of different types or frequencies (for example).

Using a priming methodology an influential study found no evidence that polysemes are processed differently to homonyms and suggested that the different senses of polysemes, like meanings of homonyms, have separate representations (Klein & Murphy, 2001). Polysemous words were visually presented twice, in phrases (e.g., “wrapping paper”); in the second presentation the sense was either consistent or inconsistent with the first meaning (e.g., “shredded paper” vs. “daily paper”) and participants performed a sensicality judgement task (in which the polysemous phrases were interspersed with foils that did not make sense, e.g., “yellow lecture”). In contrast to a model of representation where different senses share a core meaning, which would predict no effect of consistency, reaction times were facilitated by consistency and slowed by inconsistency relative to a neutral baseline. Furthermore, the size of priming effects did not interact with ambiguity type, providing no support for a difference between polysemes and homonyms (see also behavioural data of Pylkkänen et al., 2006). Recognition memory was also better for consistent senses, again evidence against a shared semantic representation and instead compatible with the existence of distinct representations for the different senses. Further evidence that polysemous senses are represented separately comes from a second study by the same authors (Klein & Murphy, 2002), which showed that volunteers did not explicitly categorise different senses of the polysemous words together. However, as Klein and Murphy acknowledge (Klein & Murphy, 2001, p. 278), their studies did not establish the type of semantic relationship between the different polysemous senses and they purposefully chose word senses that were “fairly distinct” rather than exhibiting a clear semantic overlap. This issue was addressed directly in a more recent study (Klepousniotou, Titone, & Romero, 2008) using the same paradigm as Klein and Murphy (2001). Visually presented ambiguous words were independently categorised according to the amount of semantic overlap between the different meanings into three groups: high overlap, which were mostly metonyms, low-overlap which were mostly homonyms and moderate-overlap which were a mixture of homonyms, metonyms and metaphors. Sense dominance was also manipulated. Results confirmed that sense overlap did affect reaction times to make sensicality judgements to the second presentation of ambiguous target words, and furthermore that the influence was dependent on dominance. Specifically, for dominant targets, sense consistency did not matter for those words with high sense overlap, whereas those with only moderate or low overlap resulted in faster responses when the target sense was consistent compared to inconsistent with the first presentation. For subordinate targets, responses were faster for consistent compared to inconsistent senses irrespective of the sense overlap, although accuracy for high sense overlap was not affected by consistency whereas it was for moderate and low overlap targets (Klepousniotou et al., 2008). Taken together, these effects of sense or meaning overlap are indicative of representational differences between homonyms and polysemes, and perhaps between metonyms and metaphors.

There has been little direct investigation of a potential distinction within the category of polysemes, between metaphors and metonyms. In one of just two behavioural studies exploring the possibility (Klepousniotou, 2002), participants listened to prime sentences after which they made lexical decisions to visually-presented related ambiguous words (homonyms, metonyms, or metaphors), unrelated (control) words or non-words (ISI of 0 ms). Priming (response facilitation relative to unrelated control words) was stronger for metonymic than homonymous words whereas metaphors did not differ statistically from either of the two other types (Klepousniotou, 2002). These effects were explored further in a subsequent study in which participants made lexical decisions to ambiguous target words, which were presented in isolation interspersed with unambiguous control words and non-words (Klepousniotou & Baum, 2007). For auditory presentation, responses to polysemes were faster than to homonyms and to unambiguous control words, which did not differ. Responses to metonyms were also faster than to metaphors. For visual presentation, results were less clear but nonetheless supported a distinction between metonyms and metaphors as only responses to metonyms were faster than to unambiguous controls.

1.2. The time course of meaning activation of ambiguous words

A number of behavioural priming studies have explored the time course of activation of different meanings of ambiguous words by varying the delay between the prime and the target. In one such study, which focused on homonyms, participants made lexical decisions to target words that were related to dominant or subordinate meanings of ambiguous prime words, or were unrelated (Simpson & Burgess, 1985). The delay between prime and target (stimulus onset asynchrony; SOA) was varied (16 ms – 750 ms). Results indicated access for the dominant meaning by 16 ms after stimulus onset, which by 100 ms was accompanied (although to a lesser extent) by activation of the subordinate meaning. Following activation of both meanings, the subordinate meaning decayed whilst activation of the dominant meaning was boosted again (Simpson & Burgess, 1985). In a similar study using Hebrew homonyms (SOAs of 100 ms, 250 ms, 750 ms), priming results again indicated initial activation of dominant and subordinate meanings of the ambiguous prime by 100 ms; however both were active as late as 750 ms after stimulus onset, perhaps reflecting language-specific factors (Frost & Bentin, 1992). There is also a body of evidence using the Divided Visual Field (DVF) paradigm which suggests that the time course of activation differs across the hemispheres. In one such DVF study, again using the paradigm of Simpson & Burgess (1985) (SOAs of 35 ms, 750 ms), priming results indicated that initially (35 ms) the left hemisphere showed activation of both dominant and subordinate meanings, but over time (by 750 ms) although the dominant meaning was still active, the subordinate meaning had decayed (Burgess & Simpson, 1988). These are similar results to those obtained with central presentation (see Simpson & Burgess, 1988). On the other hand, the right hemisphere takes longer (around 300 ms) to show activation of both meanings (Atchley, Burgess, Audet, & Arambel, 1996; Kovisto, 1998) and then sustains those two meanings over a longer period of time (Burgess & Simpson, 1988). Note that there is still debate regarding the exact role of context on the activation of different meanings. However, the weight of evidence suggests that although multiple meanings are activated, access and selection are strongly affected by meaning frequency and context, with the relevant meaning rapidly selected whilst contextually irrelevant meanings are suppressed or passively decay (for a review, see Morris, 2006).

The activation of polysemous senses over time has been less studied and results are not strongly conclusive. Again using a priming paradigm, one study showed activation of both dominant and subordinate polysemous senses of an ambiguous prime at 250 ms after it was presented in isolation, although only this single time point was tested (Williams, 1992). When the interpretation of the polysemous prime word was biased by a preceding sentence context, and multiple SOAs were tested, results indicated sustained activation for the alternative (contextually irrelevant) sense as late as 1100 ms after onset, but only when it was dominant (Williams, 1992). Note that this result differs to the typical short-lived activation of contextually irrelevant homonymous meanings (Morris, 2006). By contrast, when the alternative (contextually inappropriate) sense was subordinate, results were less conclusive: statistically, priming effects did not differ significantly with those for the dominant condition, but numerically, priming effects indicated only very weak activation that decayed over time (Williams, 1992).

1.3. Using MEG and EEG to investigate lexico-semantic activation

More recent research into ambiguous word processing has capitalised on the advantages of EEG and MEG methods in providing an online record of brain processing as people listen to or read words. Using MEG and a visual paradigm, Beretta and colleagues (2005) showed that the M350 brain response, which is thought to index lexical activation (Pylkkänen & Marantz, 2003)[1], peaked later in response to ambiguous homonyms relative to unambiguous controls

---

[1] Although it has been argued that the M350 is the earliest-onsetting MEG component sensitive to lexical factors (Embick, Hackl, Schaeffer, Kelepir, & Marantz, 2001), and reflects automatic lexical activation rather

and earlier in response to polysemes as the number of related senses increased. These results, which indicate faster activation as a function of an increasing number of related senses and slower activation in the case of multiple distinct meanings, are fully in support of a neuro-cognitive distinction between homonyms and polysemes.

The latency of the M350 response was also used to track lexical activation of ambiguous words in a priming study by Pylkkänen and colleagues (2006) with the stimuli of Klein and Murphy (2001). Homonyms and polysemes were presented twice in two-word phrases where the target meaning (second use of the ambiguous word "paper") was inconsistent with the prime (first use) meaning (e.g., "lined paper" – "liberal paper"). Priming effects were indexed by the M350 latency for these ambiguous targets relative to latencies for ambiguous control targets preceded by a semantically unrelated prime phrase (e.g., "military post" – "liberal paper"). Priming effects for the homonyms/polysemes were also compared to a standard semantic priming condition in which unambiguous targets ("magazine") were preceded by a semantically related prime (e.g., "lined paper" – "monthly magazine") or an unrelated prime (e.g., "clock tick - monthly magazine"). As expected, semantic priming was observed for the unambiguous targets that were preceded by a related prime relative to when they were preceded by an unrelated prime; this was realised as an earlier M350 in the left hemisphere, thought to reflect facilitated activation. Also as expected, given separate lexical entries for the prime and target meanings, homonym targets elicited a later M350 latency than their controls in the left hemisphere, reflecting inhibition of the inappropriate prime meaning. Of most interest were the results for the polysemous targets, which elicited an earlier M350 latency than their controls in the left hemisphere, thus,

---

than any post-lexical processes sensitive to decision making (Pylkkänen, Stringfellow, & Marantz, 2002) other research suggests lexical access of written words much earlier, at least by 150 ms (Hauk, Coutout, Holden, & Chen, 2012; Pulvermüller, Shtyrov, & Hauk, 2009; Sereno & Rayner, 2003).

patterning with the semantic priming effects and supporting a model in which different polysemous senses share a lexical representation. Note, however, that for some individuals, polysemous targets elicited a later M350 latency than controls in the right hemisphere in line with competition between senses.

Using EEG rather than MEG, previous research has shown that the N400 evoked brain response can be used to investigate the nature of lexical representations and semantic processing in the brain (for a review, see Kutas & Federmeier, 2011). The N400 is elicited in response to words as well as word-like and meaningful stimuli. It is larger for items that are semantically unrelated to the context, where context includes (amongst other things) word pairs, sentences, wider discourse and world knowledge. In a semantic priming paradigm, the N400 to a target word (e.g. “chair”) is reduced by a preceding prime word to which it is semantically related (e.g., “table”) compared to unrelated (e.g., “apple”), which is thought to reflect easier access to or integration of lexico-semantic information (Bentin, McCarthy, & Wood, 1985; Rugg, 1985).

Several studies have used the N400 and a priming paradigm to investigate the activation of homonyms showing that meaning dominance and context are important in determining activation patterns over time. For example, in one study (Swaab, Brown, & Hagoort, 2003), sentences were presented auditorily followed, with a delay of either 100 ms or 1250 ms, by a target word. The N400 priming effects to the target showed that the dominant meaning was active at both short and long delays irrespective of its congruence with the preceding context. By contrast, the subordinate meaning was also active at the short delay irrespective of the context, but active at the long delay only when supported by the context. In a similar study with visually presented stimuli (SOAs of 200 ms and 700 ms), activation of multiple meanings was also observed at a short delay but was restricted by context at a longer delay (Van Petten & Kutas, 1987). However, in this study meaning dominance was not manipulated and ambiguous words were all homonyms.

Most relevant to the present study is a recent investigation that used the N400 brain response to index the activation of different meanings of homonyms (balanced and unbalanced in frequency of the alternative meanings) and polysemes (metaphors and metonyms) (Klepousniotou, Pike, Steinhauer, & Gracco, 2012) and to look for evidence of a distinction between the ambiguity types. Lexically ambiguous items were presented visually (for 200 ms) as primes. After a short delay of 50 ms, target words that were either related to one of two meanings of the primes, or unrelated were presented. By assessing the extent of semantic priming, as indexed by a reduction in the N400 for related compared to unrelated targets, it was possible to conclude whether particular meanings of the primes were active and also whether activation patterns differed between the ambiguity types. For homonyms, stronger priming effects were observed for targets related to the more frequent, dominant, meaning than for those related to the less frequent meaning. This finding suggests that at a short delay, the dominant meaning is activated more strongly than the subordinate meaning, although there is still some activation of the subordinate meaning. By contrast, for metonyms, there was no difference in the extent of priming between the two related senses indicating activation of both meanings and compatible with a shared representation for metonymic senses. Metaphors, like homonyms, showed stronger priming for targets related to the dominant than subordinate meaning. However, the activation of subordinate-related meanings was also significant compared to the unrelated targets and was associated with a different topographical pattern. Unlike homonyms where the priming effect for subordinate-related meanings was larger over the left hemisphere, for metaphors, it was larger over the right hemisphere. The findings indicate hemispheric differences in the recruitment of neural resources for the activation of subordinate meanings between homonyms and metaphors, and are in line with suggestions that the right hemisphere plays a particular role in the processing of figurative meanings.

The aforementioned study provided evidence in support of a distinction between homonymous and polysemous words, and within the category of polysemy, between metaphors and metonyms. Notably, the delay between the target and the prime was very short (50 ms), and as discussed above, a number of behavioural studies have shown that the activation of different meanings of ambiguous words changes over time. It is unclear whether meanings might be sustained or might decay over time, and whether this process differs between different types of ambiguous words. For example, although evidence suggests both metonymic meanings are initially activated, suppression may differ between the meanings. And for homonyms, although activation is initially observed for both dominant and subordinate meanings, dominant meanings produce a bilateral pattern of activation whereas subordinate meanings activate predominantly a left lateralised neural pattern. However, this pattern may change over time. For example, the subordinate meaning may be more strongly activated later, which would be observable as a priming effect following a longer ISI. The proposed research aims to investigate further the time-course of meaning activation patterns by drawing on the paradigm and stimuli of Klepousniotou et al. (2012) and employing a longer delay (750 ms) between primes and targets. Presence of priming effects even at long delays would support sustained meaning activation. Moreover, any differences in the priming effects between homonymous and polysemous words would be further evidence in support of a theoretical distinction between these two types of ambiguous words.

1.4. The present study

We investigated the representation and processing of different types of lexical ambiguity, namely homonymy (balanced and unbalanced) and polysemy (metaphorical and metonymic) by using the N400 ERP brain response to index meaning activation. In a delayed visual lexical decision task, we presented ambiguous (prime) words followed after a delay of 750 ms by target words that were related to one of the meanings of the prime or unrelated. EEG was recorded and ERPs formed relative to the onset of the target word. Semantic priming effects, observable as a reduction in the N400 brain response for related targets relative to unrelated targets were taken to indicate activation of the prime meaning to which the target is related. We compared the priming effects for targets related to each of the meanings of the primes for each of the types of ambiguity.

If both meanings of a prime are activated to the same extent we should see no differences in the size of priming effects between the two related targets (relative to the unrelated target). Alternatively, the size of the priming effect may be dependent on the dominance of the prime meaning, with larger priming effects reflecting stronger meaning activation. Based on recent electrophysiological data (Klepousniotou et al., 2012) we predicted differences between semantic priming effects for homonyms and polysemes. If the activations of ambiguous meanings observed at the 50 ms delay are sustained, homonyms will show an effect of meaning dominance with greater priming effects observed for targets related to the dominant meaning compared to the subordinate meaning. Polysemes will show equivalent priming effects for targets related to the dominant and subordinate meanings. Alternatively, the pattern of meaning dominance may change over time. For example, at the later delay equivalent priming effects may be observed for targets related to the two meanings of homonyms reflecting equal activation of both meanings (note this could be either because the subordinate meaning has increased in activation or because the dominant meaning has decreased in activation). Another possibility is that no priming effects are observed because both meanings have decayed at the later time point. Thus, by presenting the targets at a long delay (750 ms) after the ambiguous prime word we will be able to draw conclusions about the maintenance of meanings as well as about processing and representational differences between homonyms and polysemes.

2. Methods

1.1. Participants

Twenty eight native British English speakers (15 female, mean age 21 years; range 18-31 years) took part in the study for course credits. Participants were right-handed based on the Briggs and Nebes inventory (Briggs & Nebes, 1975), had no speech or language difficulties, had normal or corrected-to normal vision and no record of neurological diseases. Ethical approval was issued by the Institute of Psychological Sciences, University of Leeds, and informed written consent was obtained from all volunteers. An additional 6 participants were tested and excluded from data processing and analysis for failing to complete the experiment (1 participant), for making lexical decision errors to more than 10% of the experimental target words (2 participants), for moving a lot during the recording (2 participants), for having high impedance (>25 kΩ) during the recording resulting in noisy data (1 participant).

1.2. Stimuli

Experimental stimuli comprised prime-target pairs, which were used in a previously published study (Klepousniotou et al., 2012). Thirty of each of the four types of ambiguous words were selected as primes: (1) unbalanced homonymous words (e.g., “coach”); (2) balanced homonymous words (e.g., “match”); (3) metaphorically polysemous words (e.g., “mouth”); and (4) metonymically polysemous words (e.g., “rabbit”). The ambiguous primes were nouns, although as is commonly the case with English nouns many could also be used as verbs. Each of the 120 ambiguous experimental primes was paired with three types of targets: (1) words related to the dominant meaning of the prime; (2) words related to the subordinate meaning of the prime; (3) control words unrelated to the prime. A further 120 ambiguous filler primes (30 of each of the 4 types) with similar characteristics as the experimental primes (grammatical category, number of letters and syllables) were paired with three pseudowords each (see Table 1 for examples of the experimental stimuli).

Table 1. Examples of stimuli for the four ambiguity types

Ambiguity Category	Meaning Dominance	Prime	Target		
			Dominant	Subordinate	Unrelated
Homonymy	Unbalanced (biased)	coach	bus	teach	cotton
	Balanced (equibiased)	match	mix	burn	fork
Polysemy	Metaphorical (biased)	mouth	breath	flow	rifle
	Metonymic (equibiased)	rabbit	hop	stew	chalk

Homonyms were selected from standardised lists (Gilhooly & Logie, 1980; Nelson, McEvoy, & Schreiber, 1998; Twilley, Dixon, Taylor, & Clark, 1994). For unbalanced homonyms the mean frequency of the dominant meaning was 80% (range 63-95%) and of the subordinate meaning was 14% (range 1-32%). For balanced homonyms the mean frequency of the dominant meaning was 50% (range 35-48%) and of the subordinate meaning was 41% (range 35-48%).

As there are no standardised lists of polysemes, metaphors and metonyms were chosen to exhibit specific relations between their two senses as documented in the theoretical linguistics literature (Nunberg, 1979; Pustejovsky, 1995). Of the metaphors, 10 exhibited a body part/object relation (e.g., “mouth”, referring to the organ of the body or to an aperture in nature), 10 exhibited an animal/human characteristic (e.g., “fox”, referring to the animal or to the human characteristic), and 10 exhibited an object/human characteristic (e.g., “star”, referring to the object or to the human characteristic). Of the metonyms, 10 words exhibited a count/mass relation (e.g., “rabbit”, referring to the animal or to the meat); 10 words exhibited a container/containee relation (e.g., “bottle”, referring to the container or the contents); and 10 words exhibited a figure/ground reversals relation (e.g., “cage”, referring to the structure of the cage or the space contained within).

The four types of ambiguous words were matched on mean frequency of occurrence [F(3, 116) = 0.044, p = 0.98] (Kučera & Francis, 1967): unbalanced homonyms = 43 counts per million (range 1-120); balanced homonyms = 35 (range 3-127); metaphors = 33 (range: 1-103); metonyms = 32 (range 7-119). Mean number of letters was 4.8 letters (range 3-8 letters) and did not differ between the four types of ambiguous words [F(3, 116) = 2.27, p = 0.083]. There was also no difference between word types in terms of bigram frequency [F(3, 116) = 1.96, p = 0.314] and trigram frequency [F(3, 116) = 0.17, p = 0.915].

Meaning dominance was independently established. Thirty participants who did not take part in the EEG experiment were asked to judge the relative familiarity/ frequency of each meaning/ sense of the ambiguous words using a seven-point Likert scale (1 represented rare, 7 very often). The mean familiarity ratings were: unbalanced homonymy, 5.3 (SD = 0.8) for dominant meanings and 3.4 (SD = 1.1) for subordinate meanings; balanced homonymy, 4.8 (SD = 0.9) for dominant meanings and 4.6 (SD = 1) for subordinate meanings; metaphorical polysemy, 5.8 (SD = .07) for dominant meanings and 3.4 (SD = 0.8) for subordinate meanings; metonymic polysemy, 5.3 (SD = 0.7) for dominant meanings and 5.3 (SD = 0.8) for subordinate meanings. Thus, meaning dominance was biased for unbalanced homonymy and metaphorical polysemy but equibiased for balanced homonym and metonymic polysemy. For reasons of parsimony, we retain the standard terminology “dominant” and “subordinate” even in the case of the balanced homonymy and metonymic polysemy.

Meaning/sense relatedness was also independently established. A different group of thirty participants were asked to judge the degree of relatedness of the two meanings/senses of the ambiguous words using a seven-point Likert scale (1 represented completely unrelated, 7 very related). The mean relatedness ratings were for unbalanced homonymy, 1.4 (SD = 0.2); balanced homonymy, 1.7 (SD = 0.7); metaphorical polysemy, 3.2 (SD = .05); metonymic polysemy, 6.1 (SD = 0.7). As expected, meaning/sense relatedness was low for unbalanced and balanced homonymy, moderate for metaphorical polysemy and high for metonymic polysemy.

As a final check, the classification of the stimuli as homonymous or polysemous and the dominance of the meanings, were verified by consulting standard dictionaries (such as the Wordsmyth dictionary; see also, Rodd et al., 2002). Dictionaries respect the theoretical distinction between homonymy and polysemy by listing the different meanings of homonymous words as separate entries, whereas the different senses of polysemous words are listed within a single entry. In addition, all standard dictionaries respect sense dominance by listing the central or dominant sense of polysemous words first and then providing the extended or subordinate senses.

The target words (related to the dominant or subordinate meaning of the ambiguous primes, or unrelated) were obtained from a standardized list of word association norms (Nelson et al., 1998). Importantly, target words were matched for mean frequency of occurrence [F(11,348) < 1] (Kučera & Francis, 1967): dominant-meaning related target = 31 counts per million (range 1-116); subordinate-meaning related target = 32 (range 1-121); unrelated target = 31 (range 1-126), and matched for number of letters [F(11,348) = 0.78, p = 0.65] and for number of syllables. The pseudoword targets were phonotactically legal in English and were constructed by taking real English words and replacing one or two letters. Mean number of letters was 5 (range 3-8).

In the experiment, each prime was presented visually followed by a visual target. The prime-target pairs were split into three lists. Each list comprised 120 ambiguous word experimental primes: 40 paired with dominant meaning related targets, 40 paired with subordinate meaning related targets, 40 paired with unrelated control word targets, and 120 ambiguous word filler primes paired with pseudoword targets. Thus, every participant was presented with each prime three times (once in each list) but with each target only once. Presentation of lists was counterbalanced across participants and stimuli within a list were presented in a fixed random order.

1.3. Procedure

Participants were tested individually in a single session lasting approximately one and a half hours. Stimuli were presented visually in light grey text on a black background. Each trial began with the visual presentation of a series of exclamation points (!!!) for 1000 ms, which was a signal for the participant to rest their eyes and blink. After a delay of 200 ms a fixation point (+) was presented for 500 ms to signal that the trial was about to begin. After 100 ms, the prime was presented for 200 ms followed by a delay of 750 ms and then the target for 500 ms. After a delay of 1000 ms a question mark (?) appeared for 1500 ms during which time participants had to make a lexical decision about the target (decide whether or not it was a real word in English) by pressing one of two buttons on a hand held button box (counterbalanced across participants). Participants were instructed to respond as accurately as possible; accuracy and reaction times (in ms from the onset of the "?") were recorded. After the response (or at the end of 1500 ms if the participant did not respond), there was a delay of 100 ms before the next trial started (see Figure 1). The experimental session was preceded by a practice session comprising 10 trials, which was repeated until participants could perform the task and procedure with no errors (usually one or two practice sessions were required).

Figure 1 here

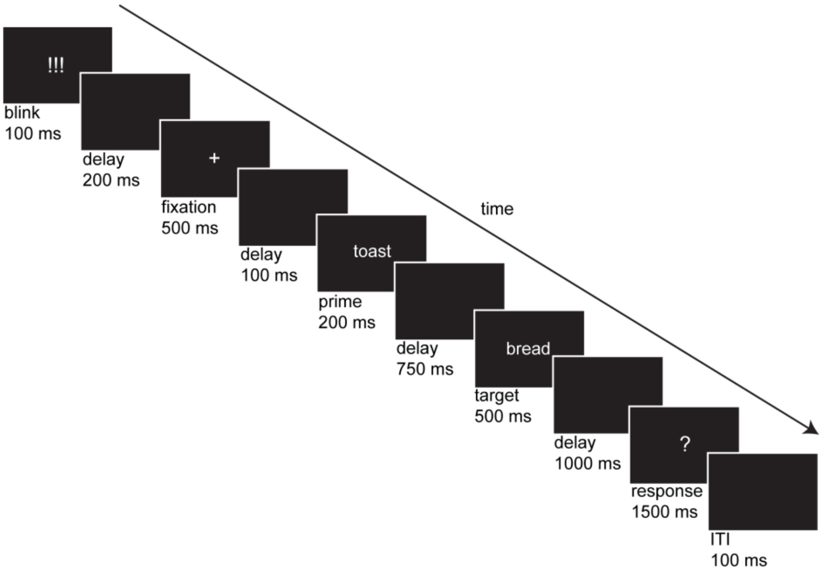

Figure 1. A single trial procedure showing timings of each stage.

1.4. EEG recording and data processing

EEG was recorded (Neuroscan Synamps2) from 60 Ag/AgCl electrodes which were embedded in a cap based on the extended version of the International 10-20 positioning system (Sharbrough et al., 1991) and fitted with QuikCell liquid electrolyte application system (Compumedics Neuroscan). Additional electrodes were placed on the left and right mastoids. Data were recorded using a central reference electrode placed between Cz and CPz. The ground electrode was positioned between Fz and Fpz. To monitor eye movements electro-oculargrams (EOGs) were recorded using electrodes positioned at either side of the eyes, and above and below the left eye. At the beginning of the experiment electrode impedances were below 10 kΩ. The analogue EEG and EOG recordings were amplified (band pass filter 0.1 to 100Hz), and continuously digitised (32-bit) at a sampling frequency of 500 Hz.

Data were processed offline using Neuroscan Edit 4.3 software (Compumedics Neuroscan). Data were filtered (0.1-40Hz, 96 dB/Oct, Butterworth zero phase filter), inspected visually and segments contaminated by muscular movement marked as bad. The effect of eye-blink artifacts was minimised by estimating and correcting their contribution to the EEG using a regression procedure which involves calculating an average blink from 32 blinks for each participant, and removing the contribution of the blink from all other channels on a point-by-point basis. Data were epoched between -100 and 900 ms relative to the onset of the experimental targets (brain response to the pseudoword targets was not analysed) and baseline corrected by subtracting the mean amplitude over the pre-stimulus interval. Epochs were rejected if participants did not make a response within the allocated time (during presentation of the “?”), or if they made an incorrect response (mean = 1.67 %) or when drift (absolute difference in amplitude between the first and last data point of each individual epoch) was greater than 100 µV. Data were then re-referenced to the average of left and right mastoid recordings and smoothed over five points so that each sampling point represents the average over the two previous and two subsequent points. Finally, further epochs were rejected when amplitude on any channel exceeded ±75 µV. Average ERPs were calculated for the target words in each of the 12 experimental conditions (4 ambiguity types x 3 target types; mean of 26 trials per condition) and grand averages calculated across participants.

1.5. EEG data analysis

To assess the processing of different types of ambiguity (unbalanced and balanced homonymy, metaphorical and metonymic polysemy) we analysed priming effects indexed by the N400 brain response. The amplitude of the ERP brain responses to the target words were compared between experimental conditions with repeated measures Analyses of Variance (ANOVAs) using the Greenhouse-Geisser correction for inequality of variance where appropriate (data are reported with corrected p values). Statistical analyses were performed on mean amplitudes over the time window of 320-420 ms, chosen to capture the maximum of the N400, based on previous studies and inspection of the data (Figures 3 and 4). We also carried out analyses over the time windows of 500-600 ms and 600-700 ms, chosen to capture a late positivity often observed following an N400, and which appeared to be present in the current data (Figures 3 and 4). To explore the data fully, ANOVAs were performed on data from midline electrodes (Midline ANOVA) and then on data from all remaining electrodes (Omnibus Lateral ANOVA), which were grouped into 12 clusters (Figure 2). Both ANOVAs included the factors of Ambiguity Category (homonymy vs. polysemy), Meaning Dominance (biased: i.e., unbalanced homonymy and metaphorical polysemy, vs. equibiased: i.e., balanced homonymy and metonymic polysemy) and Target Type (dominant vs. subordinate vs. unrelated). The Midline ANOVA included the additional factor of Site (Fpz, Fz, FCz, Cz, CPz, Pz, POz, Oz) and the Omnibus Lateral ANOVA included the additional factors of Hemisphere (left vs. right), Location (frontal vs. central vs. posterior) and Region (lateral vs. medial). Significant interactions involving the experimental conditions (Ambiguity Category, Meaning Dominance and Target) were followed up with further ANOVAs and Newman-Keuls post-hoc ($p < .05$) tests where appropriate. Only significant effects reflecting priming (effect of Target Type) and involving the experimental factors of interest (Ambiguity Category and Meaning Dominance) are reported.

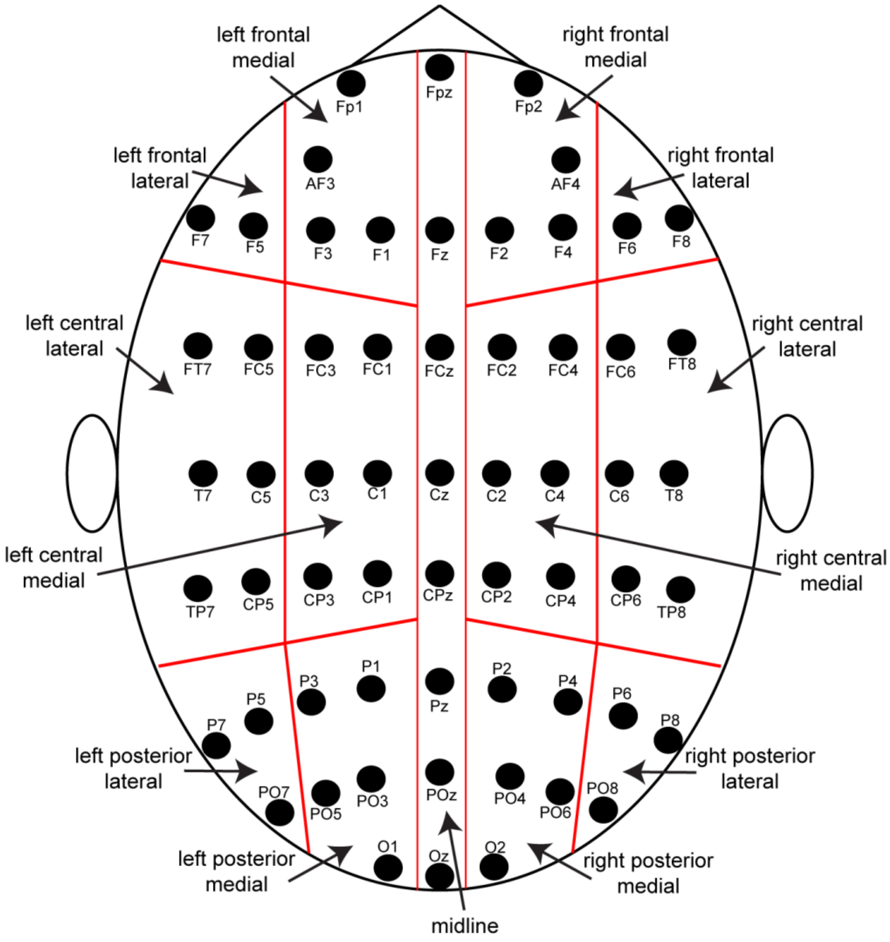

Figure 2. Approximate layout of the 60 electrodes from which data were recorded. Analyses were performed on data recorded over the midline electrodes and 12 electrode clusters (see labels).

3. Results

3.1. Behavioural data

The task was a delayed lexical decision task with an emphasis placed on accuracy and thus overall error rate was low (1.67%). Table 2 shows the mean percentage of errors for the experimental targets in the 12 conditions. An ANOVA with factors of Ambiguity Category (homonymy vs. polysemy), Meaning Dominance (biased vs. equibiased) and Target Type (dominant vs. subordinate vs. unrelated) revealed a main effect of Target [F(2,54) = 4.040, MSE = 1.455, p < .02] reflecting the overall greater error rate for unrelated than for related target words. The main effect was qualified by an interaction between Ambiguity and Target Type [F(2,54) = 3.909, MSE = 2.673, p < .04], reflecting a higher error rate for subordinate-related than unrelated targets in the metaphorical condition.

Table 2. Mean percentage error rates for the lexical decision task to the three types of targets presented following the four types of ambiguous primes

Ambiguity Category	Meaning Dominance	Target Type		
		Dominant	Subordinate	Unrelated
Homonymy	Unbalanced (biased)	1.07	1.43	1.90
	Balanced (equibiased)	0.48	1.07	3.21
Polysemy	Metaphorical (biased)	1.43	2.26	1.79
	Metonymic (equibiased)	1.19	1.67	2.74

3.2. ERP data

Figures 3 and 4 show ERPs elicited in response to the three types of target words that were presented following homonymous and polysemous prime words. In general, ERPs for all target types show a negative-going response, maximal around 370 ms over central and posterior electrodes, typical of the N400 brain response associated with activation of semantic meaning. Semantic priming effects – that is reduction in the N400 amplitude for targets that are related to the prime compared to those that are unrelated – were strongest between 320-420 ms and showed differences between experimental conditions, as explained below. Following the N400, targets elicited a positive deflection maximal around 500-700 ms (explored in two separate time windows: 500-600 ms and 600-700 ms), typical of a P600 brain response, which also showed differences between experimental conditions.

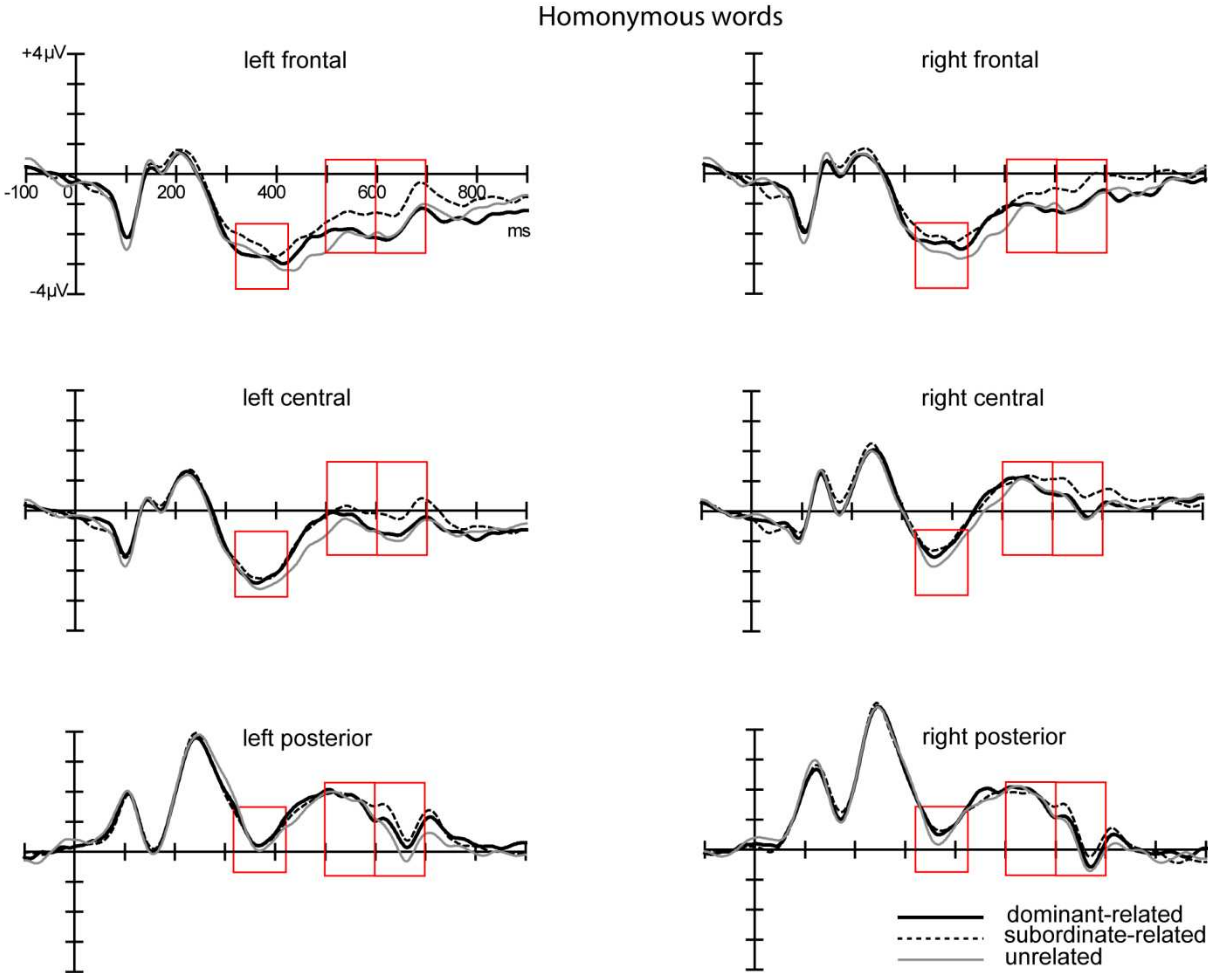

Figure 3. Grand average ERPs elicited in response to the onset of target words presented following homonymous words (balanced and unbalanced). Target words were related to the dominant (solid line) or subordinate (dotted line) meanings of the prime words or were unrelated (grey line). Data are shown for electrode clusters at frontal, central and posterior locations at the left and right hemispheres (see Figure 2). The N400 and P600 time windows are highlighted. Negative is plotted downwards.

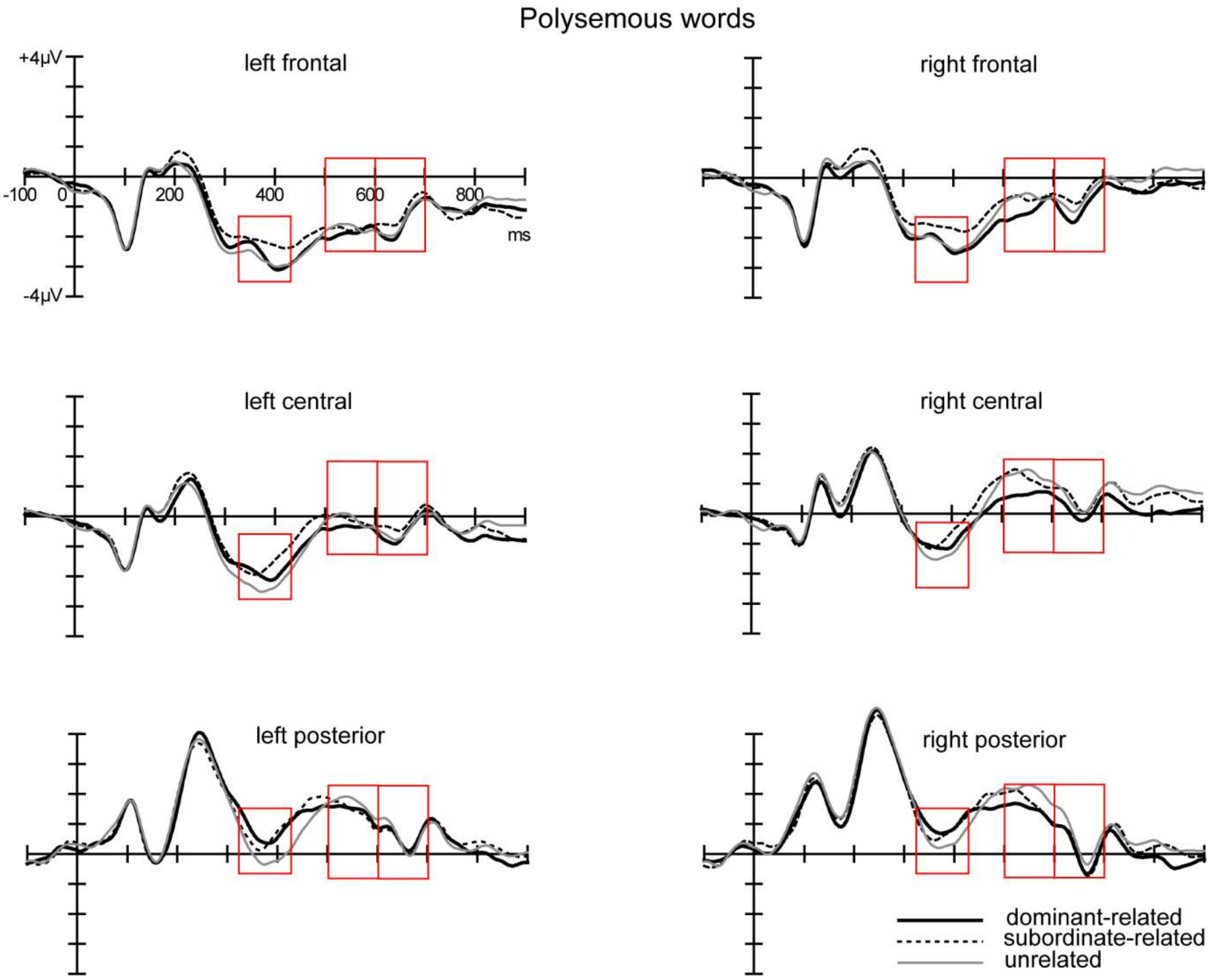

Figure 4. Grand average ERPs elicited in response to the onset of target words presented following polysemous words (metaphorical and metonymic). Target words were related to the dominant (solid line) or subordinate (dotted line) meanings of the prime words or were unrelated (grey line). Data are shown for electrode clusters at frontal, central and posterior locations at the left and right hemispheres (see Figure 2). The N400 and P600 time windows are highlighted. Negative is plotted downwards.

3.2.1. N400 analyses

In the 320-420 ms time window, the midline ANOVA with factors of Ambiguity Category, Meaning Dominance, Target Type and Site revealed a main effect of Target Type [F(2,54) = 4.073, MSE = 56.030, p < .03], and an interaction between Target Type and Site [F(14,378) = 2.240, MSE = 2.452, p < .007]. Post-hoc tests (Newman-Keuls) indicated that relative to the unrelated targets, there was a reduction in the N400 response (less negativity) for dominant-related targets ($p < .04$) and for subordinate-related targets ($p < .03$). The N400 reduction for dominant and subordinate targets was significant at FCz (dominant-related, $p <.0005$; subordinate-related, $p < .0001$), Cz (dominant-related, $p < .0006$; subordinate-related, $p < .008$), CPz (dominant-related, $p < .002$, subordinate-related, $p < .008$, and Pz (dominant-related, $p < .0006$, subordinate-related, $p < .004$) electrodes. At Fpz, only subordinate-related targets showed an N400 reduction ($p < .0002$). At Fz, both related targets showed an N400 reduction (dominant-related, $p < .00003$; subordinate-related, $p < .002$) and subordinate-related targets were also less negative than dominant-related targets ($p < .00002$). At POz, only dominant-related targets showed an N400 reduction ($p < .002$).

The omnibus lateral ANOVA with factors of Ambiguity Category, Meaning Dominance, Target Type, Hemisphere, Location and Region revealed a main effect of Target Type [$F(2,54) = 3.982$, $MSE = 51.15$, $p < .03$] and an interaction between Target Type and Region [$F(2,54) = 3.422$, $MSE = 2.475$, $p < 0.04$]. Post-hoc tests (Newman-Keuls) indicated that overall, there was a reduction in the N400 response (less negativity) for subordinate-related targets compared to unrelated targets ($p < .02$) and a trend towards a reduced N400 for dominant-related targets ($p=.08$) compared to unrelated targets, but no differences between the two related targets. The N400 reduction for related targets was significant at lateral (dominant related $p < .0001$; subordinate related $p < .0001$) and medial (dominant related $p < .001$; subordinate related $p < .0001$) regions. Subordinate-related targets showed a more reduced N400 than dominant-related targets at both lateral ($p < .01$) and medial ($p < .001$) regions.

The omnibus lateral ANOVA also revealed interactions between Ambiguity Category and Location [$F(2,54) = 4.095$, $MSE = 13.211$, $p < .05$]. Post-hoc tests (Newman-Keuls) indicated differences between homonyms and polysemes at frontal ($p < .01$) but not central or posterior locations. Most notably, there was an interaction between Ambiguity Category, Meaning Dominance, Target Type, Hemisphere and Location [$F(4,108) = 2.795$, $MSE = 2.795$, $p < .05$], indicating that the priming effects (the effect of Target) differed as a function of the type of lexical ambiguity (homonymy or polysemy) and meaning dominance (biased or equibiased). To explore the five-way interaction that involved Ambiguity Category and Meaning Dominance, separate ANOVAs were performed for the two types of lexical ambiguity, homonymy and polysemy, with factors of Meaning Dominance (biased vs. equibiased), Target Type (dominant vs. subordinate vs. unrelated), Hemisphere (left vs. right) and Location (frontal vs. central vs. parietal). Note that due to its lack of interaction with Ambiguity Category and Meaning Dominance in the omnibus ANOVA, the factor of Region was not included as a separate factor.

For both types of Homonyms (Figure 3), no effects involving the experimental conditions of interest reached significance, reflecting the absence of semantic priming for either meaning at this long delay. By contrast, for Polysemes (Figure 4) there was a significant interaction between Target Type and Location [$F(4,108) = 2.794$, $MSE = 3.573$, $p < .03$] ($p < .06$, Greenhouse-Geisser corrected) reflecting semantic priming effects which differed over the scalp location. Post-hoc tests (Newman-Keuls) revealed a reduction in the N400 response for both dominant-related and subordinate-related targets compared to unrelated targets at the central (dominant related $p < .01$; subordinate related $p < .001$) and posterior locations (dominant related $p < .001$; subordinate related $p < .009$), and for subordinate-related targets compared to unrelated targets at the frontal location ($p < .001$). Although no differences were observed between the two types of related targets at central and posterior locations, dominant-related targets were more negative than subordinate-related targets ($p < .002$) at the frontal location.

3.2.2. Late positivity analyses

In the 500-600 ms time window, the midline ANOVA with factors of Ambiguity Category, Meaning Dominance, Target Type and Site revealed an interaction between all four factors [$F(14,378) = 2.701$, $p < .0009$] but no significant post-hoc results. There was also a significant interaction between Ambiguity Category, Target Type and Site [$F(14, 378) = 4.776$, $p < .0001$]. Post-hoc tests (Newman-Keuls) showed that for homonyms, relative to unrelated targets, dominant-related targets showed greater positivity at POz ($p < .05$) but reduced positivity at Oz ($p < .005$). Subordinate-related targets showed greater positivity than dominant-related targets at Fz ($p < .03$). For polysemes, both related targets showed reduced positivity relative to unrelated targets at CPz (dominant-related, $p < .004$; subordinate-related, $p < .003$).

The lateral omnibus ANOVA with the factors of Ambiguity Category, Meaning Dominance, Target Type, Hemisphere, Location and Region showed a significant interaction between all six factors [$F(4,108)$, $p = 3.877$, $p < .006$], which we followed up by analyzing effects separately for Homonyms and Polysemes. For Homonyms, there was a significant interaction between Meaning Dominance, Target Type, Hemisphere, Location and Region [$F(4,108) = 8.358$, $p < .0001$]. Newman-Keuls post-hoc tests showed that for unbalanced homonyms there was greater positivity for subordinate-related targets relative to the unrelated targets over the left hemisphere at frontal medial ($p < .04$), central medial ($p < .006$), central lateral ($p < .03$), posterior medial ($p < .0002$), and posterior lateral ($p < .006$) electrode clusters, and over the right hemisphere at frontal medial ($p < .03$), frontal lateral ($p < .05$), and central lateral ($p < .0006$) electrode clusters. Dominant-related targets showed greater positivity than unrelated targets over the left hemisphere at central lateral ($p < .04$) and posterior lateral ($p < .002$) electrodes and over the right hemisphere at central lateral ($p < .05$) electrodes. Subordinate-related targets also showed greater positivity than dominant-related targets at right posterior lateral electrodes ($p < .004$). For balanced homonyms, greater positivity was observed over left posterior lateral electrodes for both dominant-related ($p < .0002$) and subordinate-related targets ($p < .0002$) relative to unrelated targets.

The ANOVA for Polysemes alone also showed a significant interaction between Meaning Dominance, Target Type, Hemisphere, Location and Region [$F(4, 108) = 2.858$, $p < .03$]. Post-hoc tests showed that for metaphors, subordinate-related targets showed greater positivity than dominant-related targets over left central medial electrodes ($p < .0006$). For metonyms, there was reduced positivity relative to the unrelated targets for subordinate-related targets at left posterior medial electrodes ($p < .03$) and for dominant-related targets at left posterior lateral electrodes ($p < .02$).

In the 600-700 ms time window, the midline ANOVA with factors of Ambiguity Category, Meaning Dominance, Target Type and Site revealed an interaction between Ambiguity Category, Target Type and Site [$F(14, 378) = 3.299$, $p < .0001$]. Post-hoc tests showed that for homonyms, subordinate-related targets were more positive than dominant-related targets at Fz ($p < .04$) and more positive than unrelated targets at FCz ($p < .03$). Dominant-related targets were less positive than unrelated targets at Pz ($p < .04$) and at Oz ($p < .005$).

The lateral omnibus ANOVA with the factors of Ambiguity Category, Meaning Dominance, Target Type, Hemisphere, Location and Region showed and interaction between Ambiguity Category, Meaning Dominance, Target Type and Hemisphere [$F(4, 108) = 4.718$, $p < .002$], which we followed up by analyzing the effects separately for Homonyms and Polysemes. For Homonyms, there was an interaction between Meaning Dominance, Target Type and Hemisphere [$F(2, 54) = 3.563$, $p < .04$]. Newman-Keuls post-hoc tests showed that for unbalanced homonyms over the left hemisphere there was greater positivity relative to the unrelated targets for subordinate-related ($p < .0002$) and dominant-related ($p < .02$) targets, and subordinate-related targets were more positive than dominant-related targets ($p < .0002$). For balanced homonyms over the right hemisphere, subordinate-related targets were more positive than unrelated targets ($p < .004$) and dominant-related targets ($p < .006$). For polysemes, there were no significant effects involving the factor of Target.

4. Discussion

The present study provides electrophysiological evidence for representational and processing differences between homonymy and polysemy, and informs our understanding of the time course of activation of ambiguous word meanings. Volunteers viewed ambiguous prime words, which were followed – with a delay of 750 ms – by a target word to which they made a delayed lexical decision judgement. Targets were related to one of the two meanings of the prime or unrelated, and were interspersed with pseudo-words. Most strikingly, semantic priming effects, as indexed by a reduction in the amplitude of the N400 brain response relative to unrelated targets, were observed for target words related to both meanings of polysemous prime words (both metaphors and metonyms) but not for targets related to homonymous prime words (both balanced and unbalanced). Following the N400, there was an increase in the positivity of brain responses, the timing of which is compatible with its interpretation as a P600, and the amplitude and characteristics of which differed between homonyms and polysemes. For homonyms, particularly those with more unbalanced meanings, there was greater positivity for subordinate-related (and to some extent dominant-related targets) relative to unrelated targets. The difference was present bilaterally and widespread over the scalp. By contrast, for polysemes the only indications of differences between target types were, for metonymic polysemy, in the opposite direction – a reduction in positivity for subordinate-related and dominant-related targets relative to unrelated targets that was localized over left posterior sites. Metaphorical polysemy showed a larger positivity for subordinate-related compared to dominant-related meanings over left central medial electrodes but no differences compared to unrelated targets.

4.1. Differences in the time course of processing homonymous and polysemous words

Across many studies it has been shown that the N400 is larger (more negative) for words whose meanings are more difficult to access or integrate within the context and reduced when processing is facilitated by a preceding related prime word or supporting context (for a review, see Kutas & Federmeier, 2011). The reduction in the N400 response to target words related to polysemous primes indicates that after a long delay (of 750 ms) both meanings of the prime are sufficiently activated to facilitate semantic processing of the target. By contrast, the absence of an N400 reduction for targets related to homonymous primes indicates that the meanings of these primes were not active at the long delay. Thus, the present findings indicate clear differences in the time course of processing of homonyms and polysemes.

Previous research on homonyms consistently indicated exhaustive access of both dominant and subordinate meanings within 250 ms, based on behavioural (Burgess & Simpson, 1988; Frost & Bentin, 1992; Simpson & Burgess, 1985) and electrophysiological (Atchley & Kwasny, 2003; Klepousniotou et al., 2012; Swaab et al., 2003) data, although activation patterns did show some differences due to dominance. For example, a recent ERP study (Klepousniotou et al., 2012), which used an identical paradigm to the present study but a delay of 50 ms between the prime offset and the target onset demonstrated N400 priming effects that were more widely distributed over the scalp for dominant than for subordinate meanings. This result was interpreted as reflecting activation of a richer semantic representation for dominant words. In line with this finding, behavioural priming results using the Divided Visual Field (DVF) methodology and a prime-target SOA of 35 ms also indicated activation of dominant meanings across both hemispheres but activation of subordinate meanings only in the left hemisphere (Burgess & Simpson, 1988). In terms of the pattern of meaning activation over a longer period of time, findings from previous research have been mixed. For example, one study demonstrated that 750 ms after presentation of the ambiguous word, activation was observed for both meanings (Frost & Bentin, 1992), whereas another showed activation of only the dominant meaning (Simpson & Burgess, 1985). In a third study using the DVF methodology there was activation of the dominant meaning over both hemispheres but activation of the subordinate meaning only over the right hemisphere (Burgess & Simpson, 1988). Finally, another study combining ERP recordings with the DVF paradigm indicated activation of the dominant followed by the subordinate meaning over the left hemisphere but no activation over the right hemisphere (Atchley & Kwasny, 2003). The electrophysiological data in the current study demonstrate yet another alternative pattern of results, showing that by 750 ms after prime offset (950 ms after onset) both meanings have decayed. One possible explanation is that sustained activation of the meanings of homonymous words requires more supporting context than that provided by a single word in the present experiment, particularly when the task does not require selection or retention of the meanings. Indeed ERP research shows that context has an important influence on the processing of ambiguous words. Data suggests that although both meanings are activated initially, irrespective of the context, beyond 750 ms post-ambiguity although the dominant meaning may still be active, the subordinate meaning is active only when supported by context (Swaab et al., 2003; Van Petten & Kutas, 1987). The present findings suggest that low relatedness among the meanings of homonyms (both balanced and unbalanced) strips away any chances of meaning collaboration and instead leads to meaning competition. The absence of external support from context and the continued competition between the meanings for activation eventually lead to faster decay times for both meanings.

Although context is clearly an important influence in the activation of alternative meanings of ambiguous words, particularly at a longer time lag after the ambiguity, in the present study, polysemous word meanings were still activated 750 ms after they had been presented in the absence of context. To date, there has been little research examining the time course of activation of polysemous senses, particularly for words presented in isolation. Klepousniotou et al. (2012) showed that by 250 ms after polyseme onset both dominant and subordinate senses were activated, although there was a distinction between patterns for metonymic and metaphorical polysemy. Alternative senses of metonyms showed equivalent levels of activation whereas for metaphorical polysemy activation was stronger for dominant compared to subordinate senses, and this was particularly the case over the left hemisphere in contrast to the right hemisphere where there was no effect of dominance. In the context of these findings, results from the present study, which indicate activation of all polysemous meanings by 750 ms post-offset (950 ms post-onset) and no hemispheric differences, suggest that the activation of the subordinate sense of metaphors increases over time and that the dominant metaphorical and both metonymic senses are sustained over this long period even in the absence of context. In other words, moderate and high relatedness among the senses/meanings of ambiguous words (found in metaphors and metonyms respectively) increases the probability that activation for both senses will be sustained at long delays.

The between-condition differences in the P600 observed following the N400 further corroborate differences in the time course of processing homonyms and polysemes. Several alternative functional accounts of the P600 component have been proposed. For example, the P600 is often thought to index syntactic integration and, accordingly, is mainly found in studies with sentential contexts (Kaan, Harris, Gibson & Holcomb, 2000). In the present study, there was no extended context to induce syntactic integration. However, the P600 component has also been thought to indicate re-analysis costs, with Friederici (1995), for example, claiming that it reflects repair processes following the detection of an (apparent) ungrammaticality (see also Munte, Matzke & Johannes, 1997). A slightly different interpretation of the P600 is that it reflects the cost of reprocessing with data suggesting that the more difficult it is to construct a grammatical representation, the larger the P600 (Osterhout, Holcomb, & Swinney, 1994). Finally, another yet interpretation of the P600 is that it does not reflect a purely linguistic process, but more general ‘‘surprise’’ and ‘‘context updating processes’’ (Donchin, 1981) related to the occurrence of an unexpected input (Coulson, King & Kutas, 1998; Gunter, Stowe, & Mulder, 1997). Regardless of the specific interpretation of the P600, the increased positivity, observed in particular for the target words related to homonymous primes relative to the unrelated targets, indicate difficulties in activating, processing and relating these meanings to the homonymous word primes at this long ISI. Moreover, such difficulties are compatible with our proposals, based on the N400 data, that by 750 ms after homonymous words, their alternative meanings have decayed. By contrast, the absence of an increased positivity for targets related to polysemous primes compared to unrelated targets is compatible with reduced difficulties in (both dominant and subordinate) target processing as a result of continued activation from the polysemous primes.

4.2. Representational differences between homonymous and polysemous words

The observed processing differences between homonymy and polysemy provide evidence for differential neuro-cognitive representations for the two types of ambiguity, consistent with claims made in previous studies (Klepousniotou & Baum, 2007; Klepousniotou et al., 2012; Rodd et al., 2002). Sustained activation of both meanings of polysemous words supports an account of representation in which the multiple senses are stored together. The current results do not directly address the nature of polysemous representations, but they are compatible with the possibility that polysemes exist as a basic or common, core representation, which could be seen as underspecified (Frazier & Rayner, 1990; Frisson & Pickering, 1999). The core representation comprises semantic information common across the different senses of the polysemous word (e.g., “rabbit” might include +animate, +farm animal, +edible, +meat]), which can be expanded online for complete comprehension when the context is available (or perhaps even when it is not). In the absence of contextual information or if the context is vague with respect to the appropriate interpretation, the representation could remain underspecified (Frisson & Pickering, 1999). An alternative to an underspecified polysemous representation is one that is semantically rich comprising all relevant information associated with a particular word form. Over time as more meanings are acquired the representation becomes richer. Importantly, in neither form of representation is there competition between the various senses, which instead are complementary and can co-exist and co-activate quite easily. We suggest that upon presentation of a polysemous word, the different senses act collaboratively to strengthen the representation, which facilitates the maintenance even after a long delay as in the present study.

On the other hand, the observed lack of activation of homonymous meanings in the current results is well explained by a processing mechanism in which the different meanings compete for activation (see also, Beretta et al., 2005; Rodd et al., 2002). We suggest that in the absence of a biasing context to support one meaning or the other, and the absence of a task requiring retention of either meaning, this competition results in decay of both meanings. Such an account relies on the existence of distinct neuro-cognitive representations for each of the semantically distinct meanings, which are associated with a single lexical form. Initially, very early after presentation of a homonymous word, multiple meanings are rapidly activated, although, in the absence of contextual information, dominant meanings are activated more quickly and to a greater extent (Simpson & Burgess, 1985), and their activation engages larger regions of the cerebral hemispheres than subordinate meanings (Burgess & Simpson, 1988; Klepousniotou et al., 2012). Over time, however, the alternative representations interfere with each other. In the absence of contextual cues to the contrary, the dominant meaning will be selected, whilst the subordinate meaning will be suppressed or decay (Swaab et al., 2003). Critically, we suggest the competition processes may work even to suppress/lead to decay the dominant meaning when there is no context to support its activation and task demands do not require it to be active.

The representational differences between homonymous and polysemous words, which are supported by the current study, are compatible with research that has shown differences in the time course of processing these two types of words relative to unambiguous control words. Across a number of studies it has been shown that processing words with distinct meanings delays word recognition (homonymy disadvantage) as measured by lexical decision times (Beretta et al., 2005; Rodd et al., 2002), eye fixation times (Frazier & Rayner, 1990) and the latency of the M350 brain response (Pylkkänen et al., 2006). These studies mostly interpret their results in terms of competition between the alternative meanings of homonyms[2]. On the other hand, words with multiple senses have been shown to result in faster processing (sense advantage) across a range of measures (Beretta et al., 2005; Rodd et al., 2002), which is typically accounted for by semantically richer representations relative to unambiguous words. Our findings contribute to this body of research by using neural measures to show that whilst multiple related senses of polysemous words (both metonymy and metaphors) act collaboratively to strengthen a representation, alternative unrelated

---

[2] Beretta et al., (2005) suggest that the homonymy disadvantage could also be explained by frequency rather than competition because homonyms were matched with control words on frequency of the surface form, thus the frequency of individual meanings was smaller than that of the controls. Lower frequency is known to slow word recognition.

meanings of homonymous words (both balanced and unbalanced) compete against each other. By 750 ms after ambiguous word offset (950 ms after onset) although both senses of polysemes are still active, competition has resulted in decay of both homonymous meanings.

4.3. Conclusions

The present study investigated the neuro-cognitive processing of visually-presented ambiguous words using the N400 ERP effect to index meaning activation. Semantic priming effects were observed for targets presented with a delay of 750 ms after the offset (950 ms after the onset) of polysemous primes (both metonymy and metaphors), indicating activation of both polysemous senses at this time. By contrast, semantic priming effects were not observed for homonymous words (both balanced and unbalanced) indicating that their meanings had already decayed. These processing differences, which reflect differences in meaning activation over time, also support a neuro-cognitive distinction between the representation of homonymy and polysemy. We suggest that whilst polysemous senses act collaboratively to strengthen a unified representation, the separate representations of homonymous meanings compete for activation which, in the absence of supporting linguistic context, leads to decay.

Acknowledgements

We would like to thank Jessica Levoir for assistance with data collection.

References

Apresjan, J. (1974). Regular polysemy. Linguistics 142, 5-32.

Atchley, R. A., Burgess, C., Audet, C., & Arambel, S. (1996). Timecourse, context effects, and the processing of lexical ambiguity in the cerebral hemispheres. Brain and Cognition, 30, 257-261.

Atchley, R. A., & Kwasny, K. (2003). Using event-related potentials to examine hemispheric differences in semantic processing. Brain and Cognition, 53, 133-138.

Bentin, S., McCarthy, G., & Wood, C. C. (1985). Event-related potentials, lexical decision and semantic priming. Electroencephalography and Clinical Neurophysiology, 60, 343-355.

Beretta, A., Fiorentino, R., & Poeppel, D. (2005). The effects of homonymy and polysemy on lexical access: an MEG study. Cognitive Brain Research, 24(1), 57-65.

Briggs, G. G., & Nebes, R. D. (1975). Patterns of hand preference in a student population. Cortex, 11(3), 230-238.

Burgess, C., & Simpson, G. B. (1988). Cerebral hemispheric mechanisms in the retrieval of ambiguous word meanings. Brain and Language, 33, 86-103.

Coulson, S., King, J.W., & Kutas, M. (1998). Expect the unexpected: Event-related brain response to morphosyntactic violations. Language and Cognitive Processes, 13, 21–58.

Cruse, A. D. (1986). Lexical Semantics. Cambridge: Cambridge University Press.

Donchin, E. (1981). Surprise . . . surprise? Psychophysiology, 18, 493–513.

Embick, D., Hackl, M., Schaeffer, J., Kelepir, M., & Marantz, A. (2001). A magnetoencephalographic component whose latency reflects lexical frequency. Cognitive Brain Research, 10(3), 345-348.

Frazier, L., & Rayner, K. (1990). Taking on semantic commitments: processing multiple meanings vs. multiple senses. Journal of Memory and Language, 29, 181-200.

Friederici, A.D. (1995). The time course of syntactic activation during language processing: A model based on neurological and neurophysiological data. Brain and Language, 50, 259–281.

Frisson, S., & Pickering, M. J. (1999). The processing of metonymy: evidence from eye movements. Journal of Experimental Psychology: Learning, Memory, and Cognition, 25, 1366-1383.

Frost, R., & Bentin, S. (1992). Processing phonological and semantic ambiguity: evidence from semantics priming at different {SOAs}. Journal of Experimental Psychology: Learning, Memory, and Cognition, 18, 58-68.

Gilhooly, K. J., & Logie, R. H. (1980). Meaning-dependent ratings of imagery, age of acquisition, familiarity, and concreteness for 387 ambiguous words. Behavior Research Methods, 12(4), 428-450.

Gunter, T.C., Stowe, L.A., & Mulder, G. (1997). When syntax meets semantics. Psychophysiology, 34, 660–676.

Hauk, O., Coutout, C., Holden, A., & Chen, Y. (2012). The time-course of single-word reading: evidence from fast behavioral and brain responses. Neuroimage, 60, 1462-1477.

Kaan, E., Harris, A., Gibson, E., & Holcomb, P. (2000). The P600 as an index of syntactic integration difficulty. Language and Cognitive Processes, 15, 159-201.

Klein, D. K., & Murphy, G. (2001). The representation of polysemous words. Journal of Memory and Language, 45, 259-282.

Klein, D. K., & Murphy, G. (2002). Paper has been my ruin: conceptual relations of polysemous senses. Journal of Memory and Language, 47, 548-570.

Klepousniotou, E. (2002). The processing of lexical ambiguity: homonymy and polysemy in the mental lexicon. Brain and Language, 81, 205-233.

Klepousniotou, E., & Baum, S. R. (2007). Disambiguating the ambiguity advantage in word recognition: an advantage for polysemous but not homonymous words. Journal of Neurolinguistics, 20, 1-24.

Klepousniotou, E., Pike, B., Steinhauer, K., & Gracco, V. (2012). Not all ambiguous words are created equal: an EEG investigation of homonymy and polysemy. Brain and Language, 123, 11-21.

Klepousniotou, E., Titone, D., & Romero, C. (2008). Making sense of word senses. Journal of Experimental Psychology: Learning, Memory, & Cognition, 34, 1534-1543.

Kovisto, M. (1998). Categorical priming in the cerebral hemispheres: automaticity in the left hemisphere, post-lexical in the right hemisphere. Neuropsychologia, 36, 661-668.

Kučera, H., & Francis, W. N. (1967). Computational analysis of present-day American English. Providence: Brown University Press.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). Annual Review of Psychology, 62(1), 621-647.

Lehrer, A. (1990). Polysemy, conventionality, and the structure of the lexicon. Cognitive Linguistics, 1, 207-246.

Morris, R. K. (2006). Lexical processing and sentence context effects. In M. Traxler & M. A. Gernsbacher (Eds.), Handbook of psycholinguistics (second edition) (pp. 377-401). Oxford: Elsevier.

Munte, T.F., Matzke, M., & Johannes, S. (1997). Brain activity associated with syntactic incongruencies in words and pseudo-words. Journal of Cognitive Neuroscience, 9, 318–329.

Nelson, N. J., McEvoy, C. L., & Schreiber, T. A. (1998). The University of South Florida word association, rhyme and word fragment norms. (Publication.:

http://www.usf.edu/FreeAssociation/

Nunberg, G. (1979). The non-uniqueness of semantic solutions: polysemy. Linguistics and Philosophy, 3, 143-184.

Osterhout, L., Holcomb, P.J. & Swinney, D.A. (1994). Brain potentials elicited by garden-path sentences: Evidence of the application of verb information during parsing. Journal of Experimental Psychology. Learning, Memory and Cognition, 28, 786–803.

Pulvermüller, F., Shtyrov, Y., & Hauk, O. (2009). Understanding in an instant: neurophysiological evidence for mechanistic language circuits in the brain. Brain and Language, 110, 81-94.

Pustejovsky, J. (1995). The Generative Lexicon. Cambridge, MA: MIT Press.

Pylkkänen, L., Llinás, R., & Murphy, G. L. (2006). The representation of polysemy: MEG evidence. Journal of Cognitive Neuroscience, 18, 97-109.

Pylkkänen, L., & Marantz, A. (2003). Tracking the time course of word recognition with MEG. Trends in Cognitive Sciences, 7, 187-189.

Pylkkänen, L., Stringfellow, A., & Marantz, A. (2002). Neuromagnetic evidence for the timing of lexical activation: an MEG component sensitive to phonotactic probability but not to neighborhood density. Brain and Language, 81, 666-678.

Rodd, J., Gaskell, G., & Marslen-Wilson, W. (2002). Making sense of semantic ambiguity: Semantic competition in lexical access. Journal of Memory and Language, 46, 245-266.

Rugg, M. D. (1985). The effects of semantic priming and word repetition on event-related potentials. Psychophysiology, 22(6), 642-647.

Sereno, S. C., & Rayner, K. (2003). Measuring word recognition in reading: eye movements and event-related potentials. Trends in Cognitive Science, 7(11), 489-493.

Sharbrough, F., Chatrian, G.-E., Lesser, R. P., Lüders, H., Nuwer, M., & Picton, T. W. (1991). American Electroencephalographic Society Guidelines for Standard Electrode Position Nomenclature. Journal of Clinical Neurophysiology, 8, 200-202.

Simpson, G. B., & Burgess, C. (1985). Activation and selection processes in the recognition of ambiguous words. Journal of Experimental Psychology: Human Perception and Performance, 11, 28-39.

Swaab, T., Brown, C., & Hagoort, P. (2003). Understanding words in sentence contexts: the time course of ambiguity resolution. Brain and Language, 86(2), 326-343.

Twilley, L. C., Dixon, P., Taylor, D., & Clark, K. (1994). University of Alberta norms of relative meaning frequency for 566 homographs. Memory and Cognition, 22(1), 111-126.

Van Petten, C., & Kutas, M. (1987). Ambiguous words in context: an event-related potential analysis of the time course of meaning activation. Journal of Memory and Language, 26, 188-208.

Williams, J. (1992). Processing polysemous words in context: evidence for interrelated meanings. Journal of Psycholinguistic Research, 21, 193-218.

Zgusta, L. (1971). Manual of lexicography. The Hague: Mouton.