1. Introduction

In everyday life, successful communication occurs even when we must attribute correctly a speaker’s intended meaning to words that convey a wide array of possible interpretations, that is, lexical ambiguity. Theoretical linguistics distinguishes between two types of lexical ambiguity: homonymy and polysemy. The first type of lexical ambiguity, homonymy, is observed in lexical items that “accidentally” carry two distinct and unrelated meanings2 (Weinreich, 1964). For example, in the sentences “John lay down on the bank of the river” and “The Royal Bank is the largest bank in Montreal”, the word “bank” has the meanings “river side” and “financial institution”. Homonymy is assumed to have contrastive meanings which are contradictory in nature. The context and the discourse setting help in their disambiguation selecting the appropriate meaning each time (Weinreich, 1964).

The other type of ambiguity, polysemy, involves lexical senses which relate to the same basic meaning of the word as it occurs in different contexts (Weinreich, 1964). For example, in the sentences “Mary painted the door” and “Mary walked through the door”, the word “door” in the first sentence refers to the “physical door”, whereas in the second sentence it refers to the “aperture”. Yet, the basic meaning of the word is the same in both sentences. Weinreich (1964) referred to these sense distinctions as complementary polysemy (i.e., polysemy) which, unlike senses in contrastive ambiguity, are not contradictory in nature. Rather, one sense seems more appropriate or “focused” for the interpretation of the word in the particular context.

Apart from the distinction between homonymy and polysemy, according to theoretical linguistics, there is a further distinction within polysemy into two types, which are motivated by two distinct figures of speech, namely metaphor and metonymy (Apresjan, 1974). In metaphorical polysemy, in which a relation of analogy is assumed to hold between the senses, the basic sense is literal, whereas the secondary sense was originally figurative when this metaphorically polysemous (“lip”), and metonymically polysemous words (“rabbit”) were used in a visual single-word priming delayed lexical decision task. The theoretical distinction between homonymy and polysemy was reflected in the N400 component. Homonymous words (balanced and unbalanced) showed effects of dominance/frequency with reduced N400 effects predominantly observed for dominant meanings. Polysemous words (metaphors and metonyms) showed effects of core meaning representation with both dominant and subordinate meanings showing reduced N400 effects. Furthermore, the division within polysemy, into metaphor and metonymy, was supported. Differences emerged in meaning activation patterns with the subordinate meanings of metaphor inducing differentially reduced N400 effects moving from left hemisphere electrode sites to right hemisphere electrode sites, potentially suggesting increased involvement of the right hemisphere in the processing of figurative meaning.

Event-related potentials (ERPs) were used to investigate the time-course of meaning activation of different types of ambiguous words. Unbalanced homonymous (“pen”), balanced homonymous (“panel”), metaphorically polysemous (“dog”), and metonymically polysemous words (“rabbit”) were used in a visual single-word priming delayed lexical decision task. The theoretical distinction between homonymy and polysemy was reflected in the N400 component. Homonymous words (balanced and unbalanced) showed effects of dominance/frequency with reduced N400 effects predominantly observed for dominant meanings. Polysemous words (metaphors and metonyms) showed effects of core meaning representation with both dominant and subordinate meanings showing reduced N400 effects. Furthermore, the division within polysemy, into metaphor and metonymy, was supported. Differences emerged in meaning activation patterns with the subordinate meanings of metaphor inducing differentially reduced N400 effects moving from left hemisphere electrode sites to right hemisphere electrode sites, potentially suggesting increased involvement of the right hemisphere in the processing of figurative meaning.
in meaning between the primary and the derivative meanings is not always so obvious (Apresjan, 1974).

The other type of polysemy is motivated by metonymy and a relation of contiguity or connectedness is assumed to hold between the senses. Metonymically motivated polysemy respects the usual notion of lexical polysemy, namely the ability of a word to have several distinct but related senses (Apresjan, 1974). The changes of meaning in metonymic polysemy are not accidental, as in homonymy, but systematic or “regular” (Apresjan, 1974), and both the primary and the secondary senses are quite literal. For example, the ambiguous word “rabbit” has the literal primary sense “the animal”, and the literal secondary sense “the meat of that animal”.

Drawing on the observation that homonymy and polysemy are relative concepts, it seems that some types of metaphorically motivated polysemy are closer to homonymy. On the other hand, metonymically motivated polysemy is a step further away from homonymy and possibly represents “pure” polysemy (Apresjan, 1974). Several types of metonymic changes of meaning (or shifts of meaning), which seem to hold cross-linguistically and are systematic in nature (thus, in a way, predictable and productive), have been identified such as count/mass, container/containee, producer/product, product/institution, figure/ground, and place/people alternations to name just a few (Pustejovsky, 1995).

Although polysemy is much more frequent in language, most psycholinguistic and neurolinguistic studies to date have focused mainly on homonymy (see Simpson, 1994 for a review). With respect to homonymy, most models agree that the multiple, unrelated meanings are represented separately in the mental lexicon; however, the representation of polysemy in general, and of its two subtypes – metaphor and metonymy – in particular, has been very controversial. The question we address here, using electrophysiological correlates, is how the multiple, closely related senses of polysemous words, both metaphors and metonymies, are activated and represented in the mental lexicon. Are the multiple related senses of metaphorical and metonymic polysemous words processed just like the multiple unrelated meanings of homonymous words or do they employ a qualitatively different process?

1.1. Behavioural evidence for the distinction between homonymy and polysemy

There is currently an ongoing debate in the literature, based on behavioural studies, on the representation of polysemy. On the one hand, there is evidence that the senses of polysemous words, unlike the meanings of homonymous words, are stored together in the mental lexicon. For example, words with multiple meanings associated with a single derivation (i.e., all the meanings have the same etymology) are accessed faster than words with an equal number of meanings that are associated with multiple derivations (i.e., the meanings are associated with different etymologies; Jastrzembski, 1981). In addition, several other studies suggest that homonymous and polysemous words are represented and processed differently (Frazier & Rayner, 1990; Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou, Titone, & Romero, 2008; Pickering & Frisson, 2001; Williams, 1992). For example, Frazier and Rayner (1990) found that participants’ eye movement patterns differed for polysemous and homonymous words in that polysemous words required shorter fixation times. They argued that because the meanings of homonymous words are mutually exclusive, selection of the appropriate meaning must occur before processing can proceed. In contrast, because the different senses of polysemous words are not mutually exclusive and may share a core representation, all possible meanings can remain activated so that selection and disambiguation, if necessary, is delayed. Further evidence for the facilitatory effects of the interrelatedness of multiple senses on the processing of polysemous words is observed in the processing advantage for lexical decisions for words with many senses, a trend for a disadvantage for words with many meanings (Rodd, Gaskell, & Marslen-Wilson, 2002) and the inability to suppress priming effects of the contextually irrelevant central meaning of polysemous words even over long prime-target delays (Williams, 1992).

In contrast with the notion that homonymy and polysemy are represented and processed differently, a number of experiments support the opposite view, namely that polysemy functions just like homonymy. In particular, an influential study by Klein and Murphy (2001) found no evidence that polysemous words embedded in phrasal contexts (e.g., daily paper vs. shredded paper) function differently from homonymous words (but cf. Klepousniotou et al., 2008). Their results showed that contextual consistency facilitated comprehension while contextual inconsistency inhibited comprehension. Similar findings were obtained from a series of off-line experiments as well (Klein & Murphy, 2002). Critically then, based on the findings of the studies undertaken by Klein and Murphy (Klein & Murphy, 2001, 2002), the separate representations view is supported for both homonymy and polysemy; namely, the multiple senses of polysemous words have separate representations just like the multiple meanings of homonymous words.

1.2. Behavioural evidence for the distinction within polysemy into metaphor and metonymy

As described above, polysemy is not a uniform phenomenon; rather, according to theoretical linguistics (Apresjan, 1974), polysemy is divided into metaphor and metonymy. Importantly, studies to date (Klepousniotou 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008) that exploited the distinction within polysemy into metaphor and metonymy, both in context and isolation, yielded further information about lexical ambiguity processing. In particular, in a study directly comparing homonymous, metaphorically polysemous and metonymically polysemous words, Klepousniotou (2002) found that metonymically polysemous words demonstrated stronger facilitation effects and were processed significantly faster than homonymous words, while metaphors fell somewhere in the middle between homonymy and metonymy. The distinction of metaphor and metonymy within polysemy was further supported in a set of lexical decision experiments focused on the so-called “ambiguity advantage” effect (i.e., an assumed processing advantage for ambiguous than unambiguous words) by comparing the processing of balanced homonymy, unbalanced homonymy, metaphorical polysemy, and metonymic polysemy to unambiguous frequency-matched control words (Klepousniotou & Baum, 2007). Although no processing advantage was found for homonymy (both balanced and unbalanced), a processing advantage was evident for all polysemous words – metaphorical and metonymic – (i.e., they were processed faster than unambiguous words), suggesting a “sense-relatedness advantage” effect. In addition, even in the presence of a processing advantage, metaphorically polysemous words took longer to process than metonymically polysemous words, providing further support to the theoretical linguistics division of polysemy into metaphor and metonymy.

Finally, in another study (Klepousniotou et al., 2008), participants judged whether ambiguous words embedded in word pairs (e.g., tasty chicken) made sense as a function of a cooperating, conflicting, or neutral context using the paradigm of Klein and Murphy (2001). The ambiguous words were independently rated as having low, moderate, and highly overlapping senses/meanings to map onto a homonymy to metonymy continuum. The effects of sense/meaning dominance were also examined. The results indicated...
that words with highly overlapping senses (metonymy) showed reduced effects of context and dominance compared to words with moderately or low overlapping meanings (metaphorical polysemy and homonymy), suggesting that the comprehension of ambiguous words is mediated by the semantic overlap of alternative senses/meanings.

Based on these results, it was suggested that processing differences probably indicate representational differences depending on the type of ambiguity that the words exhibit (Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008). Homonymous words show longer reaction times both in sentential contexts and isolation possibly because their multiple unrelated meanings are competing, thus slowing down the activation process. Homonymous words, then, could be seen as having several distinct mental representations in the mental lexicon and the appropriate meaning is chosen from a pre-existing, exhaustive list of senses (i.e., sense selection). Polysemous words, on the other hand, and in particular metonymous words, are processed significantly faster presumably because there is no meaning competition. This finding could indicate that for metonymous words there is only a single mental representation specified for the basic sense of the word, assigning it a general semantic value from which the extended senses are created possibly by means of lexical rules (i.e., sense creation). These findings, thus, provide evidence that homonymy and polysemy (especially metonymy) rely on distinct underlying processing mechanisms that may reflect differences in their representation. However, it is difficult to unequivocally distinguish between the two alternative views on the representation and processing of homonymy and polysemy using behavioural tests only since they tend to be more susceptible to post-lexical processes.

The choice between the alternative views on the representation of polysemy (i.e., core meaning representation versus separate representations) has important implications about the structure of the mental lexicon. If the separate representations view is accepted, then we would have multiple entries for each word, one for each meaning. On the other hand, if the opposite is true, then polysemous words would have a single entry. For this reason, using EEG methodology and focusing on the N400 component that has been shown to reflect lexical activation and semantic processing we set out to investigate whether polysemous words are represented as one word or as multiple words (like homonymous words).

1.3. Electrophysiological studies on lexical ambiguity

Most lexical ambiguity studies that used electroencephalography (EEG) and measured event-related potentials (ERPs), in particular the N400 component that marks lexical-semantic processing, have mainly focused on homonymy. In general, these studies investigated the processing of dominant-related and subordinate-related targets in single word primes (e.g., Atchley & Kwasny, 2003), word triplets (e.g., Chwilla & Kolk, 2003; Titone & Salisbury, 2004), or sentential contexts (e.g., Swaab, Brown, & Hagoort, 2003; Van Petten & Kutas, 1987). Overall, they indicate that at short ISIs, both dominant- and subordinate-related targets are (partly) activated (i.e., there are reduced effects for the N400 component), while at long ISIs, the contextually appropriate meaning is activated, with an indication that the dominant meaning is always partly activated (Swaab et al., 2003; Van Petten & Kutas, 1987). This is consistent with a weaker version of the exhaustive access model, namely the “reordered access” model (Duffy, Morris, & Rayner, 1988), according to which all meanings are activated simultaneously, at least initially, but the degree of activation depends on frequency and type of context.

More recently, two MEG studies emerged (Beretta, Fiorentino, & Poeppel, 2005; Pylkkänen, Llinás, & Murphy, 2006) that aimed to investigate the processing of lexical ambiguity. The MEG component these studies focused on is the M350 which emerges approximately 350 ms after the onset of the critical stimulus. The M350 component is considered to be equivalent to the N400 ERP component, and has been shown to mark lexical activation and semantic processing. Using MEG and a visual lexical decision task, Beretta et al. (2005) replicated the findings of Rodd et al. (2002) by showing that words with more than one meaning were accessed more slowly than words with a single meaning (i.e., they elicited later M350 peak latencies and slower reaction times). In addition, words with many senses were accessed faster than words with few senses (i.e., they elicited earlier M350 peak latencies and faster reaction times). However, as with the findings of Rodd et al. (2002), the interaction between relatedness in meaning and number of senses was not significant. Therefore, it is still not clear from these results that the processing advantage either at the behavioural or the neural level is confined to what the authors call “unambiguous words with multiple related senses” only (i.e., polysemous words).

The other MEG study, conducted by Pylkkänen et al. (2006), used the stimuli and task of Klein and Murphy (2001) asking participants to make acceptability judgements. Two-word phrases of homonymous and polysemous words were preceded either by a prime phrase that biased the opposite meaning of the ambiguous word and was considered to be the related condition (e.g., river bank – savings bank; lined paper – liberal paper) or an unrelated prime phrase (e.g., salty dish – savings bank; military post – liberal paper). They compared these phrases to phrases that were semantically related and were primed either by a related prime (e.g., lined paper – monthly magazine) or an unrelated prime (e.g., clock tick – monthly magazine) in an attempt to investigate whether the processing of polysemy involves identity or just formal and semantic similarity. The behavioural data of Pylkkänen et al. (2006) paralleled that of Klein and Murphy (2001), namely no differences were found between homonym and polysemy as in both cases related targets were responded to faster than unrelated targets. Interestingly though, for homonymous words, the MEG data (focusing again on the M350 component) showed that related targets elicited later M350 peak latencies than unrelated targets in the left hemisphere (LH), suggesting inhibition effects. On the other hand, for semantic targets, there was facilitation for related pairs for which the M350 in the LH peaked earlier than for the unrelated pairs. Polysemous words behaved similar to semantic targets, namely the M350 peaked earlier for the related targets than for unrelated targets, supporting, thus, the single lexical entry hypothesis. Pylkkänen et al. (2006) also explored sources in the right hemisphere (RH) in the same time-window (i.e., 300–400 ms) that the M350 component is found in the LH. The researchers report that only half of their subjects showed some activity in the RH. For these subjects, it was found that only polysemous words showed differential activity, with the M350 peaking later for related targets than for unrelated targets. Based on this finding, Pylkkänen et al. (2006) suggested that there may be competition among the senses of polysemous words in the RH. Although this is an interesting finding given the patient literature on lexical ambiguity that suggests that patients with RH damage have problems in the interpretations of metaphorical meanings (e.g., Brownell, 1988; Klepousniotou & Baum, 2005b), it is difficult to assess it given that the precise type of stimuli the researchers used is not known. Nevertheless, judging from the stimuli of Klein and Murphy (2001), the researchers must have used a wide variety of polysemous words, conflating both metaphorically and metonymically motivated polysemy. It is possible then that the (limited) effects observed in the RH are driven by the items that have more metaphorical interpretations.
Further evidence about increased contributions from the right hemisphere in the interpretation of metaphorical meanings comes from divided visual field (DVF) studies showing that at short ISIs, both literal and metaphorical meanings are facilitated in the LH, with metaphorical meanings also being facilitated in the RH. At longer ISIs, only literal meanings are facilitated in the LH, whereas only dominant meanings are activated in the RH. At longer ISIs, only dominant meanings are activated in the LH, whereas both dominant and subordinate meanings are activated in the RH. These findings indicate that the cerebral hemispheres are differentially involved in the activation, selection and suppression of ambiguous word meanings (Burgess & Simpson, 1988; Chiarello, Maxfield, & Kahan, 1995), and suggest that closely related items are activated and maintained in the LH, while the RH subserves more distantly related words (consistent with Beeman’s (1998) coarse semantic coding hypothesis).

2. Experiment

The present experiment aimed to investigate the temporal patterns of meaning activation of different, well-controlled, types of lexical ambiguity, namely homonymy (both balanced and unbalanced) and polysemy (both metaphorical and metonymic), in order to shed more light on the way that words with multiple meanings or multiple senses are processed and represented in the mental lexicon. In the present experiment, the ambiguous words were used as primes because the hypothesized differences in their lexical representations are predicted to be revealed by specific differences in the resulting N400 effects for related relative to unrelated target words. In particular, for homonymous words that have distinct unrelated meanings (e.g., bank-money vs. bank-river), reduced priming effects (leading to increased N400 effects) were expected for subordinate meanings relative to dominant meanings when compared to unrelated targets (possibly with a more left-lateralized scalp distribution which would be consistent with behavioural studies using the DVF methodology at short ISIs such as Burgess & Simpson, 1988; Chiarello et al., 1995). On the other hand, for polysemous words that have multiple related senses (e.g., rabbit-hop vs. rabbit-stew), increased priming effects (leading to reduced N400 effects) were expected for both dominant and subordinate meanings relative to unrelated targets, supporting the notion of a core meaning representation (possibly with more bilateral scalp distribution; see Anaki et al., 1998 for similar findings in a behavioural study using the DVF methodology).

2.1. Experimental methods

2.1.1. Participants

Eighteen native speakers of English (nine male and nine female) with an average age of 24.4 years (range 19.3–29.11) and an average of 17.3 years of education (range 12–25) participated in the study. All participants were right-handed (as assessed by the Brigs & Nebes, 1975 handedness inventory), they were free of speech-language and hearing disorders and had normal or corrected to normal (20/20) vision.

2.1.2. Materials

Prime-target pairs representing four distinct types of lexical ambiguity were constructed in the following way. Thirty of each of the four types of ambiguous words were selected as primes: (1) unbalanced homonymous words (e.g., “coach”; one meaning is more frequent (dominant) than the other meaning (subordinate)); (2) balanced homonymous words (e.g., “panel”; both meanings are equally frequent); (3) metaphorically polysemous words (e.g., “mouth”); and (4) metonymically polysemous words (e.g., “rabbit”).

Unbalanced and balanced homonymous words were chosen from standardized lists of ambiguous words (e.g., Gilhooly & Logie, 1980; Nelson, McEvoy, Walling, & Wheeler, 1980; Twilley, Dixon, Taylor, & Clark, 1994). For the unbalanced homonymous words, the frequency of occurrence of the dominant meaning was never less than 63%, and the frequency of occurrence of the subordinate meaning was never greater than 32%. Overall, the dominant meaning had a mean frequency of occurrence of 80% (range: 63–95%) and the subordinate meaning had a mean frequency of 14% (range: 1–32%). The average frequency of occurrence of the unbalanced homonymous words was 34 (range: 1–120) (Francis & Kucera, 1982).

For the balanced homonymous words, the frequency of occurrence of the dominant meaning was never less than 41%, and the frequency of occurrence of the subordinate meaning was never greater than 48%. Overall, the dominant meaning had a mean frequency of occurrence of 50% (range: 41–59%) and the subordinate meaning had a mean frequency of 41% (range: 35–48%). The average frequency of occurrence of the balanced homonymous words was 35 (range: 3–127) (Francis & Kucera, 1982).

As there are no standardized lists of metonymous and metaphorically polysemous words, these were chosen to exhibit specific relations between their two senses as documented in the theoretical linguistics literature (Pustejovsky, 1995). In order to investigate the effects of a broader range of words with metonymical and metaphorical meaning extensions, multiple types of metonymical and metaphorical words were included. In particular, metonymical words exhibited the following types of metonymic relations: 10 words with the count/mass relation (e.g., “rabbit”, referring to the animal or the meat); 10 words with the container/containee relation (e.g., “bottle”, referring to the container or the contents); and 10 words with the figure/ground reversals relation (e.g., “cage”, referring to the structure of the cage or the space contained within). The mean frequency of occurrence for the metonymically polysemous words was 32 (range: 7–119) (Francis & Kucera, 1982).

Similarly, metaphorical words exhibited three types of metaphorical relations, namely 10 body part/object words (e.g., “mouth”, referring to the organ of the body or an aperture in nature), 10 animal/human characteristic words (e.g., “fox”, referring to the animal or the human characteristic), and 10 object/human characteristic words (e.g., “star”, referring to the object or the human characteristic). The average frequency of occurrence of the metaphorically polysemous words was 33 (range: 1–103) (Francis & Kucera, 1982).

Meaning dominance for all ambiguous words was also independently established through a rating study on meaning familiarity/frequency using a seven-point Likert scale (where one represented rare and seven very often). A different set of 30 participants (all native speakers of English) were asked to judge the relative familiarity/frequency of each meaning/sense of the ambiguous words. The mean familiarity ratings were: unbalanced homonymy, 5.3 (SD: 0.8) for dominant meanings and 3.6 (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: 0.7) for dominant meanings and 3.4 (SD: 0.8) for subordinate meanings; metonymyc 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 equi-biased for balanced homonymy and metonymic polysemy. It should be noted that for the sake
of parsimony, we retain the standard terminology “dominant” and “subordinate” to refer to the two meanings/senses of balanced homonymy and metonymic polysemy.

The classification of all stimuli as homonymous, metonymous or metaphorical was also verified by consulting standard dictionaries (see also Rodd et al., 2002). All such dictionaries respect the distinction between homonymy and polysemy by listing the different meanings of homonymous words as separate entries, whereas the different senses of metonymous and metaphorical words are listed within a single entry. In addition, all standard dictionaries respect sense dominance by listing the central or dominant sense of metonymous and metaphorical words first and then providing the extended or subordinate senses. Finally, all ambiguous words were matched for frequency of occurrence \(F(3,116) = 0.044, p = 0.98\) (Francis & Kucera, 1982), syllable and letter length \(F(3,116) = 2.27, p = 0.083\) with mean letter length of 4.8 letters (range: 3–8), bigram \(F(3,116) = 1.96, p = 0.314\) and trigram frequency \(F(3,116) = 0.17, p = 0.915\), and grammatical category (i.e., all words and meanings were predominantly nouns).

Four types of targets were used: (1) words related to the dominant meaning of the ambiguous word primes; (2) words related to the subordinate meaning of the ambiguous word primes; (3) control words unrelated to the ambiguous word primes; and (4) legal non-words. Word associates were obtained from a standardized list of word association norms (Nelson, McEvoy, & Schreiber, 1998) and were matched for frequency of occurrence \(F(11,348) = 0.061, p = 0.99\) (Francis & Kucera, 1982), syllable and letter length \(F(11,348) = 0.78, p = 0.65\). In particular, word associates to the dominant meaning had a mean frequency of 31 (range: 1–116), word associates to the subordinate meaning had a mean frequency of 32 (range: 1–121), and unrelated control words had a mean frequency of 31 (range: 1–126). Examples of the experimental stimuli are presented in Table 1.

Target non-words were created by taking real words of English and replacing one or two letters. All the non-words that were created were phonotactically legal and had a mean letter length of 5 (range: 3–8).

In the experiment, each word prime was followed either by a target word related to its dominant meaning, a target word related to its other (subordinate) meaning, an unrelated control target word, or a non-word. Non-words were presented following prime words that had the same characteristics as the experimental prime words (e.g., ambiguity type, syllable length, grammatical category, etc.) but were not part of the experimental prime word groups.

Each testing session consisted of three lists. Each list contained 40 ambiguous word primes followed by dominant meaning related word targets, 40 ambiguous word primes followed by subordinate meaning related word targets, 40 ambiguous word primes followed by unrelated control word targets, and 120 filler ambiguous words that had the same characteristics as the experimental prime word groups. For each word target, an unrelated control word target was also used. The list was counterbalanced and trials within a list were presented in fixed random order.

2.1.3. Procedure

All participants were tested in a single session that lasted approximately one and a half hours. Participants were tested individually, seated in a comfortable position in a dimly lit room, facing a colour computer monitor approximately 100 cm away. Each trial began with the visual presentation of a series of exclamation points (!!!) on the computer screen for 1000 ms to allow the participants to rest their eyes and blink. After a delay of 200 ms, a fixation point (+) was presented on the screen for 500 ms. The fixation point (+) indicated to the participants that they should stop blinking and that a stimulus was about to be presented. After 100 ms, the prime was presented for 200 ms, and 50 ms later the target was presented for 500 ms. Following a delay of 1000 ms, a question mark (?) appeared on the screen for 1500 ms indicating to the participants that they had to make a lexical decision about the target. Participants were instructed to respond as accurately as possible using the mouse keys by pressing the YES key if they thought the target was a real word in English, and the NO key if they thought it was a non-word. Reaction times (in ms) and accuracy rate were recorded by the computer.

Reaction times were recorded from the onset of the question mark cue until the participant responded. If the participant did not respond within 1500 ms, the trial was recorded as a non-response, and the next trial was presented after a delay of 100 ms. A practice session of 10 trials preceded the presentation of the actual experiment. If the participants did not understand the task, they blinked during the presentation of the stimuli, or responded before the presentation of the question mark, the practice session was repeated until the participant was trained and was clear about what the task required.

2.2. EEG recording

The electroencephalogram (EEG) was recorded from 64 pin-type active Ag–AgCl electrodes mounted in a headcap (arranged according to the extended 10–20 International system) and connected to an ActiveTwo AD-box (Biosemi, Amsterdam). Recording sites included 10 midline electrodes (FPz, AFz, Fz, FCz, Cz, CPz, Pz, Oz, Iz) and 27 electrodes over each hemisphere (P1/P2, Fp1/Fp2, AF3/AF4, AF7/AF8, F1/F2, F3/F4, F5/F6, F7/F8, FC1/FC2, FC3/FC4, FC5/FC6, T7/T8, C1/C2, C3/C4, C5/C6, T7/T8, CP1/CP2, CP3/CP4, CP5/CP6, TP7/TP8, P1/P2, P3/P4, P5/P6, P7/P8, P9/P10, PO3/PO4, PO7/PO8, O1/O2). Two midline electrodes (CMS and DRL) between Cz and CPz served as the ground electrodes. Bipolar horizontal EOG was recorded between electrodes at the outer right and left canthi. Bipolar vertical EOG was recorded between electrodes above and below the participant’s left eye. Electrode impedance was kept below 5 KΩ. The signals were recorded continuously with a bandpass filter of 0.16–100 Hz and digitized at a sampling rate of 512 Hz. Digital codes were sent from the stimulus presentation computer to mark the onset and type of each target stimulus.

2.3. Analyses

The BrainVision Analyzer software (Brain Products GmbH) was used to analyze the EEG data off-line. First, the EEG was re-referenced to the algebraic average of the right and the left mastoids. Then, the EEG was segmented into epochs starting 350 ms before and ending 1500 ms after the presentation of the target. Event-related potentials were computed for each condition by averaging across trials of the same type, time-locked to the target word. A baseline interval prior to target presentation (−100 to 0 ms) was used to normalize the onset voltage of the ERP waveform. Trials

<table>
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<tr>
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<th>Subordinate</th>
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containing ocular artifacts (detected using the Gratton & Coles algorithm; Gratton, Coles, & Donchin, 1983) and amplifier saturation artifacts (±200 μV) were excluded from the averages. Given that participants were trained to minimize blinking and to blink only at specific times, the number of EOG-contaminated trials was extremely low (less than 7% of all trials) and therefore such trials were rejected from further analyses as suggested in the literature (Handy, 2005;Luck, 2005; see also Steinhauer, Drury, Portner, Walenski, & Ullman, 2010 for a similar approach to ocular artifact rejection in reading studies). The main ERP component implicated in semantic priming to date is the N400. In order to describe the onsets and length of the ERP effects, the latency window between 350 ms and 450 ms, which clearly incorporates the N400 maximum, was used to statistically evaluate the data.

Only correct responses given after the cue (i.e., the presentation of the question mark – ?) to real word targets were analyzed. Prior to statistical analysis, early responses (i.e., responses given before the presentation of the cue, comprising 1.74% of the data) and errors (1.49% of the data) were removed. Repeated measures analyses of variance (ANOVA) were conducted separately for the midline electrodes (Omnibus Midline ANOVA) and for the lateral electrodes (Omnibus Lateral ANOVA) with Ambiguity category (two levels: homonymy, polysemy), Meaning dominance (two levels: biased, equibiased), and Target type (three levels: dominant-related, subordinate-related, unrelated) as factors. The Midline ANOVA included the additional factor Electrode (nine levels: Fpz, AFz, Fz, FCz, Cz, Pz, POz, Oz, Iz; CPz was excluded because it malfunctioned for the majority of participants). The Lateral ANOVA included the additional factors Hemisphere (two levels: left, right), Site (three levels: anterior, central, posterior), and Region (two levels: lateral, medial). When evaluating the Electrode, Site and Target type factors (which included more than one degree of freedom), the Greenhouse–Geisser correction was applied (corrected p-values are reported).

3. Results

3.1. Behavioural data

Error rates for each condition are presented in Table 1. Given that the paradigm employed a delayed reaction time task, accuracy to real word targets was high. The error data were subjected to a repeated measures ANOVA with Ambiguity category (two levels: homonymy, polysemy), Meaning dominance (two levels: biased, equibiased), and Target type (three levels: dominant-related, subordinate-related, unrelated) as factors. There was only a significant main effect of Target type \(F(2,34) = 3.78, \text{MSE} = 8279, p < 0.05\), indicating that participants made more errors to unrelated than related targets.

3.2. ERP data: 350–450 ms

Event-related potentials for relevant contrasts are displayed in Figs. 1a–4. As a general pattern, the various conditions did not vary during the first 300 ms after target word onset. Systematic priming effects – and differences between priming conditions – are strongest between 350 and 450 ms, especially at central and posterior electrodes, consistent with previous reports of N400 modulations in ERP priming studies.

3.2.1. Omnibus midline ANOVA

The midline analysis yielded a significant main effect of Target type \(F(2,34) = 7.31, \text{MSE} = 131.329, p = 0.01\) and a significant two-way interaction of Electrode \(\times\) Target type \(F(16,272) = 3.91, \text{MSE} = 6.478, p < 0.01\). Post-hoc tests (Newman–Keuls, \(p < 0.05\)) revealed that N400 effects were more negative for unrelated targets compared to both dominant- \((p < 0.005)\) and subordinate-related \((p < 0.005)\) targets which did not differ from each other \((p = 0.7)\), while the post hoc tests for the Electrode \(\times\) Target type interaction revealed that these effects were maximal at electrodes Cz \((p < 0.00005)\) and Pz \((p < 0.00005)\), consistent with the literature, while weaker effects were also apparent at electrodes FCz \((p < 0.005)\) and POz \((p < 0.005)\).

3.2.2. Omnibus lateral ANOVA

Only relevant effects involving factors that reflect the experimental manipulations (i.e., those involving Ambiguity category and Target type) will be reported. Largely mirroring the effects at the midline, there was a significant main effect of Target type \(F(2,34) = 4.59, \text{MSE} = 112.088, p < 0.05\) as well as significant two-way interactions of Site \(\times\) Target type \(F(4,68) = 4.02, \text{MSE} = 18.281, p < 0.05\), and Region \(\times\) Target type \(F(2,34) = 3.69, \text{MSE} = 10.446, p < 0.05\). As confirmed by follow-up analyses (Newman–Keuls, \(p < 0.05\)), these interactions reflected the fact that, overall, N400 priming effects were larger over posterior \((p < 0.005)\) and central \((p < 0.05)\) than frontal electrodes \((p = 0.7)\), and more prominent at medial \((p < 0.0005)\) than lateral electrodes \((p < 0.005)\).

A significant Site \(\times\) Meaning dominance \(\times\) Target type interaction \(F(4,68) = 3.19, \text{MSE} = 5.984, p < 0.05\) reflected the following expected differences between biased and equibiased words, especially at posterior electrodes: For biased ambiguous words (across conditions), reduced N400 amplitudes due to priming were observed only for dominant-related \((p < 0.0005)\), but not for subordinate-related targets \((p = 0.2)\). In contrast, equibiased ambiguous words showed equal N400 priming effects for both dominant- \((p < 0.0005)\) and subordinate-related \((p < 0.0005)\) targets. Note, however, that this overall pattern for biased versus equibiased ambiguous words varied across subconditions (for details see below).
There was also a three-way interaction of Region × Ambiguity category × Target type [F(2, 34) = 4.27, MSE = 12.962, p < 0.05], which was qualified by a more significant four-way interaction of Hemisphere × Region × Ambiguity Category × Target type [F(2, 34) = 7.90, MSE = 1.781, p < 0.01]. Finally, there was also a significant Hemisphere × Ambiguity category × Meaning dominance × Target type interaction [F(2, 34) = 4.11, MSE = 7.792, p < 0.05]. Unlike the various effects reported above, these latter four-way interactions pointed to processing differences between the two categories of lexical ambiguity, homonymy and polysemy. More specifically, they suggested that both (i) the strength of the semantic relatedness (Target type) and (ii) the combination of target type and the prime’s relative bias towards one meaning (Meaning dominance) pointed to different neurocognitive processing mechanisms in homonymy and polysemy. In order to explore the underlying patterns in more detail, separate ANOVAs were performed for each category of lexical ambiguity (i.e., Homonymy and Polysemy). Note that the four-way interactions in the omnibus lateral ANOVA reported above only allowed us to examine the following two 3-way interactions within each category: (1) Hemisphere × Region × Target type and (2) Hemisphere × Meaning dominance × Target type.

3.2.3. Homonymy ANOVAs

Homonyms did indeed show a significant Hemisphere × Region × Target type [F(2, 34) = 3.67, MSE = 0.132, p < 0.05] interaction. Subsequent post hoc tests (Newman–Keuls, p < 0.05) revealed an important underlying pattern: for dominant-related targets, a strong priming effect (reducing the N400 amplitude) was significant across both hemispheres, for both medial (left hemisphere and right hemisphere).
The present study used event-related potentials (ERPs) to investigate the time-course of activation of homonymous and polysemous ambiguous words. We focused on the N400 component of the ERPs that reflects semantic processing and integration and is most pronounced for semantically incongruous/unrelated stimuli (e.g., Atchley & Kwasny, 2003; Chwilla & Kolk, 2003; Swaab et al., 2003; Titone & Salisbury, 2004; Van Petten & Kutas, 1987). Given the evidence that N400 effects are reduced for semantically congruous or semantically related stimuli, differential processing patterns were expected to emerge for subordinate meanings/senses of homonymous and polysemous words. In particular, it was predicted that the N400 component will be clearly reduced for the dominant meanings of homonymous words, but it would be more pronounced for the less expected, subordinate meanings (especially for unbalanced homonymous words). On the other hand, for polysemous words, based on previous behavioural findings (e.g., Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008), we assume that the core meaning hypothesis holds. As such, we expected the N400 component to be reduced for both dominant and subordinate senses given that they are semantically interrelated and, thus, simultaneously activated. In addition, we further expected a division to emerge within polysemous words, between metaphor and metonymy (see also Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008).

4. General discussion

Differences in the relative frequency of the multiple meanings of homonymous words did not seem to differentially influence
processing patterns. For homonymous words (both balanced and unbalanced), dominant-related targets showed reduced N400 effects indicating effects of dominance/frequency. Relatively reduced N400 effects were also observed for subordinate-related targets; however, these were confined predominantly to left hemisphere electrode sites, possibly pointing to limited involvement from the right hemisphere in the processing of subordinate meanings in homonymy. It seems that for dominant meanings the full set of the semantic representation (distributed across both hemispheres) is activated leading to more robust priming effects. In contrast, for subordinate meanings only a subset of the semantic representation (distributed predominantly over the left hemisphere) is activated leading to weaker priming effects (consistent with behavioural findings using the DVF methodology; see Burgess & Simpson, 1988; Chiarello et al., 1995). It is possible then that longer ISIs are required for the activation of the full set of the semantic representation of subordinate meanings in homonymy (assumed to be distributed across both hemispheres). The present findings are consistent with earlier studies investigating N400 patterns for homonymous words (Artechle & Kwasny, 2003; Swaab et al., 2003) and indicate that at short ISIs there seems to be exhaustive meaning activation but the degree of activation depends on frequency and type of context (consistent with the "reordered access" model proposed by Duffy et al., 1988).

On the other hand, for polysemous words (both metaphors and metonymies), both dominant- and subordinate-related targets showed reduced N400 effects relative to unrelated targets. These effects held across electrode sites over both hemispheres pointing toward effects of core meaning representation, in concert with previous behavioural findings (e.g., Klepousniotou, 2002; Klepousniotou & Baum, 2007), as well as an ERP study with older adults (Taler, Klepousniotou, & Phillips, 2009). A significant difference between dominant- and subordinate-related targets was further attested only in metaphor. Using neural correlates, it was shown for the first time that although the N400 effects were comparable for dominant- and subordinate-related targets in metonymy, in metaphor, there was a scalar effect in that dominant-related targets showed a stronger N400 priming effect (smaller N400 amplitudes) relative to subordinate-related targets as well, especially over the left hemisphere. Over the right hemisphere, subordinate-related targets in metaphor showed almost the same large priming effect as dominant-related targets.

These findings point to differential involvement of the neural generators underlying the processing of homonymy and polysemy. Although it is impossible to directly link the scalp distribution of ERPs to a specific anatomical structure, our findings of a more bilateral N400 effect for polysemous (and increased right-lateralized N400 priming effects for the subordinate senses in metaphor) are certainly compatible with the hypothesized stronger involvement of the right hemisphere in the representation and processing of the subordinate meanings in metaphor (Beeman, 1998) and corroborate the neurolinguistic findings from lesion studies (Klepousniotou & Baum, 2005a; Klepousniotou & Baum, 2005b) regarding the involvement of the left and right cerebral hemispheres in the appreciation and resolution of lexical ambiguity.

4.2. Implications for the mental representation of homonymy and polysemy

The present findings have important implications for the nature of the mental representations of ambiguous words, as well as for models of lexical processing. They point towards differential representations for homonymous and polysemous words, consistent with the suggestions of earlier studies (e.g., Klepousniotou & Baum, 2007; Rodd et al., 2002). Polysemous words (and in particular metonymy) seem to occupy one end of the continuum, in terms of their representation, with their multiple interrelated senses stored together; homonymous words occupy the other end of the continuum with their unrelated meanings being stored separately (and competing for activation).

For homonymous words, the present results suggest that they have several distinct mental representations, one for each of their multiple and unrelated meanings (e.g., Jastrzembski, 1981; Klepousniotou, 2002; Rubenstein, Garfield, & Millikan, 1970). As Klepousniotou (2002) discussed, homonymous words are assumed to have multiple semantic representations which are associated with a single phonological/orthographic representation in the mental lexicon. The different meanings of homonymous words are represented separately in the lexicon. Thus, homonymous words are understood by selecting their intended meaning from a (presumably exhaustive) list of potential meanings, requiring the process of sense selection. In other words, in homonymy, the ambiguity is already established in the mental lexicon and the different meanings of the word pre-exist; they are stored separately and they are selected when required. Given that one word form is associated with multiple semantic representations, when a homonymous word is encountered, its multiple unrelated meanings are competing for activation. This competition presumably affects negatively the word recognition process and could explain the reduced priming effects observed in the present study. Neural generators responsible for N400 effects over the left hemisphere were particularly involved in the processing of homonymy and in the presence of short ISIs, as the one used in this experiment, there is evidence that both meanings may be activated to a certain degree (see also Artechle & Kwasny, 2003; Swaab et al., 2003), yet there is still a distinct preference for the most dominant meaning (even when the relative frequencies of the two meanings are very similar).

With respect to polysemous words, the present results indicate that only a basic sense with general specifications about the meaning of the word (i.e., a single, semantically rich representation) may be assumed to be stored in the lexicon, consistent with the suggestions of previous behavioural studies (Klepousniotou, 2002; Klepousniotou & Baum, 2007). The extended/subordinate senses, which are closely related to the basic sense, are generated (presumably on-line) from the basic sense. Neural generators responsible for N400 priming effects over both the left and the right hemisphere were involved in the processing of polysemous words. Having only a single representation in the mental lexicon, polysemous words (and in particular metonymic words which are assumed to represent "pure" polysemy) do not have to undergo the process of ambiguity resolution that might compromise the activation process suggesting that both dominant and subordinate meanings are processed simultaneously and to a similar degree. These findings are consistent with previous studies using eye-tracking methodology (e.g., Frazier & Rayner, 1990; Frisson & Pickering, 1999) that reported effects of immediate interpretation with faster reading times associated with polysemous words.

4.3. Resolving the debate on polysemy: representation differences between metonymy and metaphor

The present findings help resolve a long-standing debate in the polysemy literature regarding the representation of polysemous words (i.e., whether polysemous words are processed and represented like homonymous words). Previous behavioural studies provided mixed results with some researchers reporting differences between homonymy and polysemy (e.g., Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008; Rodd et al., 2002) and others reporting similar processing (e.g., Klein & Murphy, 2001; Klein & Murphy, 2002). The present study
not only corroborates the findings of two recent MEG studies (Beretta et al., 2005; Pylkkänen et al., 2006) in demonstrating differences at the neuronal level between homonymy and polysemy, but crucially it extends further these results by showing an important difference within polysemy that may explain the disparities in previous findings. In particular, the present study is the first to demonstrate a difference between the two types of polysemy at a neuronal level. Although both metaphor and metonymy show a processing advantage (i.e., reduced N400 for both dominant and subordinate meanings compared to unrelated meanings), there is a clear difference between the two not only at a behavioural but also at a neurophysiological level. More specifically, although the N400 component was reduced for both dominant- and subordinate-related targets relative to unrelated targets for both metonymy and metaphorical polysemy, there was a difference between dominant and subordinate N400 effects for metaphorical polysemy only. In other words, although for metonymy, dominant and subordinate targets showed equivalent reduced N400 effects relative to unrelated targets, there was a graded effect for metaphor. Dominant targets in the metaphor condition exhibited reduced N400 effects compared to subordinate targets, and both dominant and subordinate targets exhibited reduced N400 effects compared to the unrelated targets, drawing the distinction between metaphor and metonymy. It is possible then that previous studies that did not control carefully for the type of polysemy (i.e., conflating metonymy and metaphorical words) obtained mixed results.

This leads us to the representational possibilities for metaphorically polysemous words. According to theoretical linguistics, metaphor is a subdivision of polysemy; one might assume, then, that there should be a single core meaning representation in the mental lexicon, in parallel to what exists for metonymy words. Earlier behavioural studies, however, have shown that although metaphor is grouped under polysemy, it seems to lie somewhere between “pure” homonymy and “pure” polysemy (Klepousniotou, 2002; Klepousniotou & Baum, 2007; Klepousniotou et al., 2008). For example, Klepousniotou (2002), using a cross-modal priming task, showed that metonymic words had significantly greater priming effects and were processed significantly faster than homonymous words, while metaphors lay somewhere in the middle and were not statistically different from either homonymous or metonymy words. The present electrophysiological findings are in agreement with the theoretical linguistics literature which holds that metaphorically motivated polysemy seems to be quite unconstrained and irregular in nature, in the sense that the referent of the subordinate meaning is not always predictable (e.g., Apresjan, 1974; Pustejovsky, 1995). There are cases, where the senses are sufficiently related, but there are also cases, where the relatedness in meaning is not so obvious. It seems that metaphorically polysemous words do not have a fixed status in the lexical ambiguity continuum, but rather may be in a transition phase from generated senses to separately stored senses. For example, although sets of words for which metaphorical extensions hold can be identified, like body parts that can be used to refer to objects, the relations that hold between the dominant and subordinate senses are not necessarily predictable (in contrast to metonymic shifts that are predictable and productive; Apresjan, 1974). Of course, there are cases, where the primary and the derivative meanings keep a sufficiently large part in common, but there are also cases, where the relatedness in meaning is not so obvious, creating perhaps the need for more contextual information. The present electrophysiological findings seem to indicate that the representation of metaphor is differently distributed than both metonymy and homonymy and requires increased contributions from distinct neural generators, possibly in the right hemisphere, especially in the computation of the subordinate, figurative senses.

5. Conclusion

The data reported here investigated the activation patterns of dominant and subordinate meanings/senses of different types of lexical ambiguity, namely homonymy (balanced and unbalanced) and polysemy (metonymy and metaphor). Focusing on the N400 component of the event-related potentials, which has been shown to index lexical access and semantic integration, it was found that for homonymous words (both balanced and unbalanced) predominantly dominant-related targets showed reduced N400 amplitudes, indicating effects of dominance/frequency. In contrast, for polysemous words (both metaphors and metonymies), it was found that both dominant- and subordinate-related targets showed reduced N400 relative to unrelated targets, pointing toward effects of core meaning representation. Furthermore, an important division within polysemy, previously demonstrated behaviourally (e.g., Klepousniotou & Baum, 2007) was demonstrated for the first time using EEG methodology. Although the N400 effects were comparable for dominant- and subordinate-related targets in metonymy across hemispheres, for metaphor there was a graded effect, whereby the N400 effects were reduced for dominant-related targets relative to subordinate-related targets relative to unrelated targets; the difference between dominant- and subordinate-related targets being more pronounced over the left hemisphere but relatively reduced over the right hemisphere, possibly indicating increased right hemisphere contributions to the processing of figurative meanings in metaphor.

Acknowledgments

This research was supported by a Postdoctoral Fellowship from the Centre for Research on Language, Mind and Brain to the first author and by a grant from the Canadian Institutes of Health Research (CIHR) to the senior author. We would like to thank Pascale Tremblay for help with EEG methodology and Marie-Eve Rivard for help with testing.

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