

Short Communication

Sentence context affects the brain response to masked words

Seana Coulson*, David Brang

University of California, San Diego, United States

ARTICLE INFO

Article history:

Accepted 23 February 2010

Available online 19 March 2010

Keywords:

N400

Masked priming

Semantic priming

ABSTRACT

Historically, language researchers have assumed that lexical, or word-level processing is fast and automatic, while slower, more controlled post-lexical processes are sensitive to contextual information from higher levels of linguistic analysis. Here we demonstrate the impact of sentence context on the processing of words not available for conscious report by recording ERPs as sentences ended congruously or incongruously. Sentence final words were either masked to prevent their conscious identification, or were unmasked. For both masked and unmasked words, congruous completions elicited less negative ERPs than incongruous ones between 300 and 500 ms after word onset (N400). Relative to the unmasked words, congruity effects in masked words were much smaller, began slightly later, and displayed a more anterior distribution. Results suggest contextual priming effects indexed by the N400 component reflect both automatic and controlled processes. Data are interpreted as suggesting a link between the neural generators of the N400 and conceptual short-term memory, a dynamic process for conceptual activation and structuring that is triggered by perceptual input.

© 2010 Elsevier Inc. All rights reserved.

1. Introduction

For several decades now, language researchers have distinguished between lexical and post-lexical processes in which lexical processing involves the retrieval of linguistic information associated with a given word, and post-lexical processing involves the combination of word level information with other information needed to update the overall message-level representation of the text or discourse (for a review see Brown, Hagoort, and Kutas (2000)). Further, lexical processes have been characterized as being fast, automatic, and purely facilitative; post-lexical processes are slower, more controlled, and capable of both facilitation and inhibition (Posner & Snyder, 1975). At the level of semantics, or meaning, lexical processing is typically conceptualized as involving the spread of activation in a network of word representations (Neely, 1991), while post-lexical processing involves an array of processes sensitive both to general background knowledge and to local knowledge about the situation at hand.

A crucial component of this distinction is that sensitivity to sentence context is confined to slower, controlled post-lexical processes. Lexical processing can be facilitated by the prior presentation of a related word (e.g. “doctor” preceded by “nurse”) – a phenomenon known as semantic priming – but not by sentence context. Indeed, Forster (1976, 1981) has argued forcefully against

the influence of sentential context on lexical processing, because it would seem to require the storage of links between a finite set of word representations and a potentially infinite number of sentence contexts. Similarly, Taft (1994) writes “While it is easy to envisage a lexical memory system set up in such a way that associated words are linked together, it is less obvious how lexical memory would be set up to allow sentence fragments to be linked to associated words.”

The classic approach to word recognition stands in contrast to more interactive approaches that posit contextual influences at multiple levels of linguistic analysis, including the recognition of both spoken (Allopena, Magnuson, & Tanenhaus, 1998; Elman & McClelland, 1986; Gaskell & Marslen-Wilson, 1997) and written (Grainger & Jacobs, 1996; McClelland & Rumerlhart, 1981) words. Often grounded in biologically plausible computational architectures, interactive models describe word recognition as a constraint satisfaction process in which information at multiple levels of linguistic structure (e.g. phonology, syntax, and semantics) is applied simultaneously. Such models maintain traditional distinctions between lexical and post-lexical processing, but view contextual factors as affecting all levels. Whereas traditional models posit a series of discrete processing stages, interactive models point instead to cascaded processing in which even high level discourse information can affect lexical processing.

An important issue in the cognitive neuroscience of language thus concerns the automaticity of the processes underlying the N400 component in the event-related brain potential (ERP). A negative-going potential observed between 300 and 500 ms after the onset of a meaningful stimulus, this component is perhaps the

* Corresponding author. Address: Department of Cognitive Science, University of California, San Diego, 9500 Gilman Dr., Dept. 0515, La Jolla, CA 92093, United States. Fax: +1 (858) 534 1128.

E-mail address: coulson@cogsci.ucsd.edu (S. Coulson).

most studied physiological manifestation of language comprehension (for review see Lau, Phillips, and Poeppel (2008)). The initial report of the N400 was as a brain response sensitive to sentential congruity, being larger for anomalous sentence completions than for expected ones (Kutas & Hillyard, 1980). Subsequent research has suggested it reflects the brain's default response to a meaningful stimulus, as it is elicited by words, linguistic signs, co-speech gestures, pictures, and even videos of actions (for review see Wu and Coulson (2005)). Further, N400 amplitude is highly correlated with measures of predictability in a sentence context (DeLong, Urbach, & Kutas, 2005).

Given its sensitivity to sentential context, most language researchers have assumed that the N400 reflects post-lexical processes (Chwilla, Brown, & Hagoort, 1995; Holcomb, 1988). However, the N400 response to words presented in lists has been modulated by factors long-associated with lexical processing, such as word frequency (Smith & Halgren, 1989), repetition (Rugg, 1985), orthographic legality (Kutas & Hillyard, 1980), and association (Bentin, McCarthy, & Wood, 1985; Holcomb, 1988). Further, N400 priming effects have been reported under a number of conditions thought to discourage controlled processes. For example, N400 priming effects have been observed with non-semantic tasks (Besson, Kutas, & Petten, 1992; Kutas & Hillyard, 1989), and when the proportion of related primes and targets was low (Holcomb, 1988), suggesting they do not depend on participants' strategies. N400 priming effects have also been observed when short stimulus onset asynchronies (SOAs) obtained between primes and targets (Anderson & Holcomb, 1995; Besson, Fischler, Boaz, & Raney, 1992; Boddy, 1986), suggesting they reflect a fast-acting automatic process.

Such findings have led some investigators to suggest that N400 effects in words and sentences alike reflect lexical processing (Kutas & Federmeier, 2000). On this view, N400 amplitude is sensitive to lexical-level variables such as word frequency and word association because it represents brain activity subserving word-level processing. According to the lexical account, context effects on the N400 are mediated by predictive processing that yields the graded activation of orthographic, phonological, and conceptual features of upcoming words. Although the N400 itself reflects the activation and selection of lexical information, the predictive processing that mediates N400 context effects exploit word-level associations, as well as sentence and discourse contexts. On the lexical view, N400 sentence congruity effects do not result because it is easier to integrate a congruous completion into the context. Rather, congruous sentence contexts pre-activate features of the target word that facilitate lexical processing. The automaticity of the N400 thus has implications for the influence of context on lexical processing, and the support it would imply for interactive models of language processing.

One way to investigate the issue of automaticity involves the use of masked priming (Forster & Davis, 1984). In this paradigm, a briefly (e.g. 50 ms) presented prime word is preceded by a pattern mask (such as a series of consonants), and followed either by another mask, or by the target word. The combination of the brief presentation duration with the masks prevents the subject from consciously perceiving the prime. Any observed facilitation of the target stimulus, then, is attributed to the automatic processes initiated by the brief presentation of the prime. Masking is typically interpreted as preventing processes that engage conscious perception of the prime, thus limiting its processing to automatic components. This interpretation is supported by neuroimaging data indicating that many of the same brain regions are activated in the processing of masked versus unmasked words, but that the level of activation is reduced by masking (Dehaene et al., 1998).

Brown and Hagoort (1993) report the first use of the masked priming technique to address the automaticity of the N400. Using

a between-subjects design, these investigators measured semantic priming either with reaction times or the amplitude of the N400 for word pairs in which the prime stimuli either were or were not presented with visual masks. Brown and Hagoort (1993) found semantic priming effects on reaction times using masked and unmasked primes, but N400 effects only when utilizing unmasked stimuli. Citing their failure to find N400 priming effects with masking, Brown and Hagoort concluded that the N400 component does not index automatic lexical processes, but rather, controlled post-lexical ones. However, subsequent investigators have reported reliable masked priming effects on the N400, using both repetition priming (Misra & Holcomb, 2003; Schnyer, Allen, & Forster, 1997) and semantic priming (Deacon, Hewitt, Yang, & Nagata, 2000; Holcomb, Reder, Misra, & Grainger, 2005; Kiefer, 2002).

Here we tested whether automatically processed words are subject to contextual priming mechanisms indexed by the N400 component in the ERP. To do so, we recorded ERPs as participants read supra-liminally presented sentence contexts that ended either with a masked word or an unmasked one (see Fig. 1). Sentence final words were either predictable from the sentence

Stop signs are bright red (green)

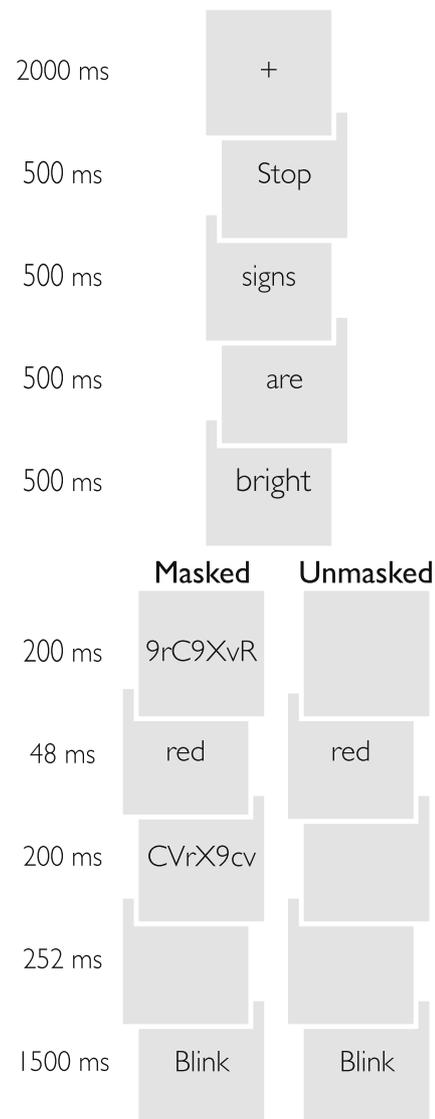


Fig. 1. Example trial illustrating the sequence and timing of events.

context (congruous completions), or comprised incongruous completions of the preceding sentence fragment. Congruous and incongruous completions were all relatively short, frequent, and highly imageable terms from the same category (colors). If contextual priming mechanisms indexed by the N400 operate only under controlled processing, N400 congruity effects would be expected for unmasked words, but not for masked words. If contextual priming mechanisms involve a combination of automatic and controlled processes, N400 congruity effects would be expected to be present in either case, but larger for unmasked words which are subject to conscious identification than for masked words which are not.

2. Methods

2.1. Participants

Data in both studies were collected from the same 16 right-handed, native English participants, ranging in age from 18 to 24 (mean age = 20.1 years, $SD = 1.8$), and including 12 women. Handedness was assessed via the Edinburgh Inventory (Oldfield, 1971), which yields a laterality quotient ranging from +1 (strongly right-handed) to -1 . All participants were right-handed, yielding an average laterality quotient of $+0.74$. All participants gave signed informed consent prior to the experiment, and participated in fulfillment of a course requirement. None of the participants reported any past or current neurological or psychiatric disorders.

2.2. Discrimination study

2.2.1. Materials and procedure

To discern each subject's ability to correctly perceive masked and unmasked sentence final words, we devised a behavioral discrimination task administered immediately after ERP recording. Subjects were presented with two color words in quick succession, and instructed to press the right button if the color words were the same (RED red) and the left button if they differed (RED blue). Fifty percent of trials included backward and forward masks surrounding the second color word.

This task was intended to provide a fairly strong test of participants' ability to perceive masked words under conditions that were similar to those in the ERP experiment. Just as our sentence contexts allowed participants to anticipate the (congruous) sentence final word, the suprathreshold prime word in the behavioral task allowed them to anticipate the (repeated) probe. Moreover, participants were not asked to identify probe words, but merely to indicate whether or not they were the same as the prime. It is thus possible to perform above chance on the repetition judgment without being able to fully read the probe words.

Trials were initiated with a fixation cross for 1000 ms, followed by a suprathreshold prime word (RED, ORANGE, YELLOW, GREEN, BLUE, PURPLE) for 400 ms, either a blank screen or mask (9rC9XvR) for 200 ms, the target word (red, orange, yellow, green, blue, purple) for 48 ms, either a blank screen or mask (CVrX9cv) for 200 ms, and a blank screen for 800 ms. Data were analyzed as d -prime values to reflect each subjects' sensitivity to repetition.

2.3. ERP study

2.3.1. Materials and procedure

Stimuli consisted of 360 sentences ending either with a predictable, contextually congruous color term ("The Coca-Cola logo is white and red"), or with an incongruous color term ("green"). These sentences have been used in prior work in our laboratory,

and were known to elicit robust N400 congruity effects among healthy adults in our participant pool (Brang, Edwards, Ramachandran, & Coulson, 2008; Brang, Kanai, Ramachandran, & Coulson, *in press*). Congruity of sentence final words was established in a separate normative study in which at least 30 people were given sentence contexts minus the target word and asked to complete the sentence. The cloze probability of a particular target word is the percentage of participants who produced that word on this production task. The cloze probability of congruous targets was 76.8%, and was 2.6% for incongruous targets.

The Edinburgh Associative Thesaurus was used to retrieve lexical associates of all target words. Sentence contexts were subsequently searched for the presence of those associates. If we examine the entire sentence context, congruous targets were more often preceded by lexical associates than incongruous targets (74% versus 59%). However, restricting our attention to the two-word window necessary for automatic priming, lexical associates were present for 43% of congruous and 36% of incongruous targets. In view of previous findings that suggest lexical priming is negligible in constraining sentence contexts such as those used in the present study (Coulson, Federmeier, Petten, & Kutas, 2005; Traxler, 2000), it was determined that this very slight imbalance in lexical associates was unlikely to modulate N400 amplitude.

Multiple stimulus lists were employed so that while no individual participant saw the same sentence twice, across participants each sentence ended an equal number of times with congruous/incongruous endings. Experimental sessions were comprised of 10 blocks containing 36 sentences each. Half of the sentences in each block ended as expected (congruous completions), and half with an unexpected color word (incongruous completions). Furthermore, half of the congruous and incongruous endings in each block were immediately preceded by and followed by a visual mask.

All participants were seated in a comfortable chair at a distance of 37 in. from the monitor in a sound-attenuated room. Sentences were visually presented one word at a time at the rate of two words per second. All words were presented in black against a grey background. Sentence final words in the masked condition were preceded by a visual mask ("9rC9XvR") lasting 200 ms; the sentence final word was presented immediately after the offset of the mask for 48 ms, and immediately followed in turn by a mask ("CVrX9cv") lasting 200 ms; finally a blank screen was presented for 252 ms, followed by a "blink" command (Fig. 1). Sentence final words in the unmasked condition were preceded by a blank screen lasting 200 ms, the sentence final word presented immediately thereafter for 48 ms, followed by a blank screen for 452 ms; the word "blink" then appeared for 200 ms followed by a blank screen for 1300 ms to remind the participant to blink.

Participants' task was to silently read each word, and to refrain from eye movements from the time the sentence-final stimulus appeared until the "blink" command was presented. They were told that all sentences would end with a word, but that we had programmed the computers to make it difficult to read some of the words. Participants were thus instructed that sentences would end either with an expected or unexpected word, and that the final word would sometimes be difficult to read.

Testing sessions began with a 10 trial practice block containing both masked and unmasked trials. Practice trials were intended to train participants to comply with eye movement restrictions, and to give them the opportunity to clarify task instructions. The practice trials were repeated if requested by the participant, or if they blinked more than twice during the presentation of sentence final words. The experimental trials were initiated once the experimenter had judged that the participant understood the task and the (somewhat unnatural) eye movement restrictions.

2.3.2. Electroencephalographic and electro-oculographic recording

Participants' electroencephalogram (EEG) was monitored with a commercial electrode cap with 29 scalp sites arranged according to the International 10–20 system. Horizontal eye movements were measured with a bipolar derivation of electrodes placed at the outer canthi. Vertical eye movements and blinks were monitored with an electrode under the right eye. All electrodes were referenced on-line to the left mastoid and all impedances were maintained below 5 k Ω . The EEG at a band pass of 0.01 and 100 Hz was amplified with SA Instruments 32-channel bioamplifiers, digitized at 250 Hz, and stored on a computer hard disk for later averaging.

2.3.3. Analysis of ERPs

ERPs were time locked to the onset of the sentence-final stimuli, and signals were averaged with a time window of –100 to 920 ms around an event; the 100 ms period preceding the onset of the target item served as the baseline. These parameters are typical for ERP studies using language stimuli similar to those in the present study (see Kutas, Federmeier, Staab, and Kluender (2007) for a review). Epochs containing blinks, eye movements, amplifier drift, or blocking were rejected prior to averaging. ERPs were measured and analyzed using customized software, similar to that used in studies reported by Kutas and Federmeier (2000). Unless noted otherwise, analysis involved peak amplitude measurements of each participant's ERPs elicited between 200 and 300 ms post sentence-final stimulus onset (intended to capture the P2 component), and mean amplitude measurements between 300 and 500 ms post sentence-final stimulus onset (the latency window typically used to capture the N400 component; Kutas et al., 2007). The P2 effect was an unexpected result, and thus the latency window was determined post hoc. Analysis of the P2 was, however, very similar to that employed by other ERP studies using sentence materials (e.g., Wlotko & Federmeier, 2007).

Measurements were subjected to repeated measures ANOVA, with the within subject factors of Condition (masked/unmasked), Congruity (congruous/incongruous), and Electrode Site (FP1, FPz, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, C3, Cz, C4, TP7, CP3, CPz, CP4, TP8, T5, P3, Pz, P4, TP7, O1, Oz, O2). Although the original degrees of freedom have been maintained for clarity, where appropriate, *p*-values were subjected to Greenhouse–Geisser correction (Greenhouse & Geisser, 1959). Scalp-distribution maps highlight the N400 component at 392 ms.

3. Results

Relative to incongruous sentence completions, ERPs to congruous words were more positive in the P2 latency range, and less negative in the N400 window (see Fig. 2). Analysis of the N400 revealed a main effect of Congruity [$F(1, 15) = 40.79, p = .000$], qualified by an interaction with Condition [$F(1, 15) = 16.04, p = .001$]. Follow-up analyses indicate the interaction results because the congruity effect was much larger for unmasked stimuli (approximately 3.6 μ V) than for masked stimuli (0.6 μ V). Although the effect size was quite small in the latter condition, sentence congruity was statistically significant both for the unmasked (Congruity [$F(1, 15) = 33.78, p = .000$]; Congruity * Electrode [$F(28, 420) = 3.59, p = .018$]) and the masked (Congruity [$F(1, 15) = 7.66, p = .014$]) words. N400 amplitude was thus reduced for congruous relative to incongruous stimuli irrespective of masking. However, the effect size was larger for unmasked than masked words, and visual inspection suggests the unmasked congruity effect was more broadly distributed over the scalp (see Fig. 2).

Analysis of the P2 revealed a reliable congruity effect [Congruity $F(1, 15) = 9.83, p = .007$] which did not differ as a function of condition [Condition * Congruity $F(1, 15) = 0.75, p = .401$; Condi-

tion * Congruity * Electrode $F(28, 420) = 0.52, p = .736$]. Because the P2 is a centrally distributed component, follow-up analyses were conducted on medial and midline electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4, O1, Oz, O2). These analyses revealed a reliable 1.0 microvolt congruity effect in the unmasked condition [$F(1, 15) = 8.00, p = .013$], and a marginal 0.6 μ V congruity effect in the masked condition [$F(1, 15) = 4.30, p = .056$]. For both masked and unmasked stimuli, the amplitude of the P2 was slightly enhanced for words that were congruous sentence completions relative to incongruous ones.

Performance on the discriminability study suggested participants were able to consciously perceive the words in the unmasked but not the masked condition (see Fig. 3). Analysis of d' scores revealed participants' better sensitivity in the unmasked than the masked condition [Condition $F(1, 15) = 83.45, p = .000$]. Follow-up analyses revealed that subjects could reliably detect word-pair congruity in the unmasked condition [One sample t -test $t(15) = 9.68, p = .000$] but not in the masked condition [One sample t -test $t(15) = 1.08, p = .30$], thus suggesting participants ability to read briefly presented words was reliably above chance for unmasked, but not for masked stimuli. Analysis of the relationship between congruity effect size and d' revealed no evidence of a correlation for the P2 congruity effect in either the masked (Pearson $R = .35, t(14) = 1.40, p = .18$) or the unmasked (Pearson $R = .09, t(14) = 0.35, p = .73$) condition. Likewise, there was no evidence of a correlation between d' and the size of the N400 congruity effect for masked words (Pearson $R = .06, t(14) = 0.25, p = .80$) or unmasked words (Pearson $R = .15, t(14) = 0.56, p = .59$).

4. Discussion

To test whether unconsciously processed words are subject to contextual priming mechanisms reflected in the N400 component, we recorded ERPs as healthy adults read sentences such as "Stop signs are bright" that ended either congruously ("red") or incongruously ("green"). As expected, when sentence final words were presented without masks, congruous completions elicited less negative ERPs between 300 and 500 ms post-onset than incongruous ones, suggesting a facilitative effect of context on the processing of congruous sentence completions. Moreover, a similar pattern of ERP effects was observed even when sentence final words were masked: congruous completions elicited reliably less negative ERPs between 300 and 500 ms post-onset than incongruous ones. However, contextual priming effects were smaller for masked (0.6 μ V) than for unmasked (2.5 μ V) words, and displayed a more focal scalp topography (see Fig. 2). In addition, for both masked and unmasked stimuli, congruous words elicited a slightly larger (0.8 μ V) P2 component 200–300 ms post-onset than did incongruous words.

Overall, these data suggest that contextual priming indexed by the N400 component includes both automatic and controlled processes. In showing the contribution of automatic processes to the N400, results of the present study contrast with an earlier report that masked priming yielded effects on reaction time measures without accompanying N400 effects (Brown & Hagoort, 1993). As previously noted, however, those null results may have been partially attributable to limitations in the power of the design employed (for critique see Deacon et al. (2000)). Moreover, a number of groups have subsequently reported reliable N400 effects to words preceded by masked primes (Deacon et al., 2000; Holcomb et al., 2005; Schnyer et al., 1997).

Results of the present study are also in keeping with those reported by Stenberg, Lindgren, Johansson, Olsson, and Rosen (2000). As in the present study, Stenberg and colleagues recorded ERPs to a masked target preceded by a fully visible prime. Using

Stop signs are bright

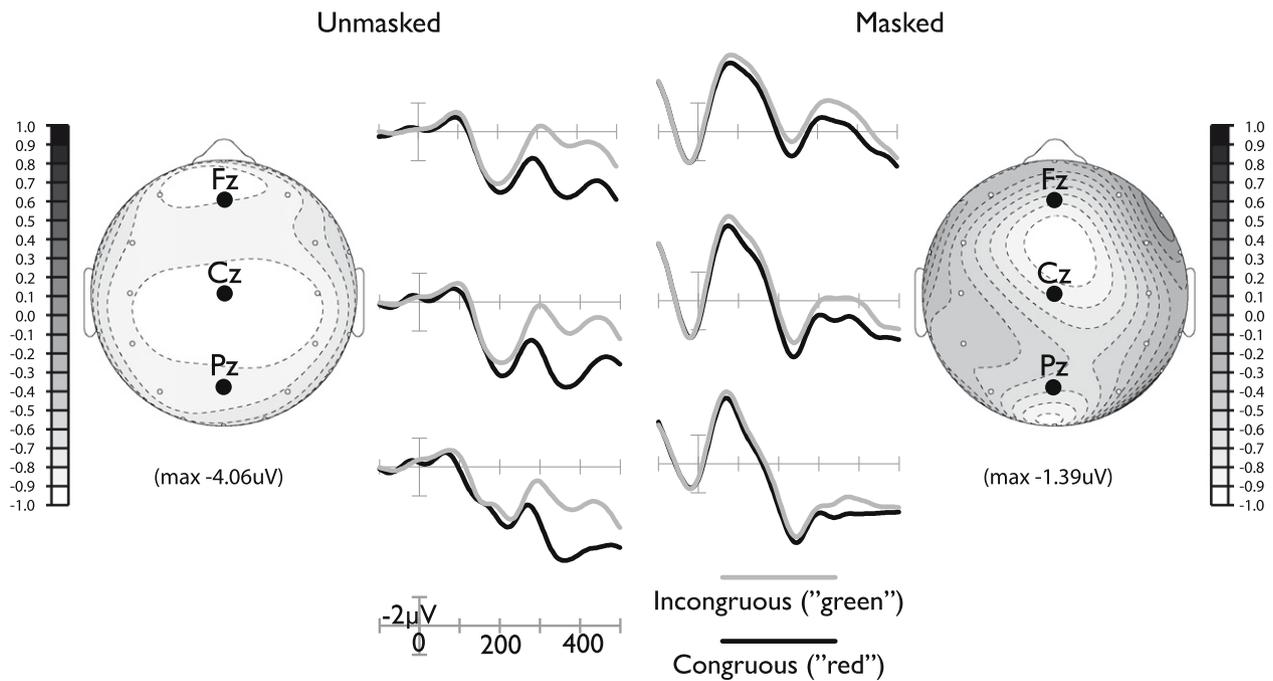


Fig. 2. Center: grand-average event-related potentials at midline electrodes Fz, Cz, and Pz to masked/unmasked congruous (black line) and incongruous (grey line) sentence final words. N400 amplitude between 300 and 500 ms was larger for incongruous compared to congruous words. Periphery: spline-interpolated topographic maps showing the scalp distribution of the N400 congruency effect, derived by subtracting the waveform elicited by congruous sentence final words from incongruous sentence final words. The sentence congruency effect was focally distributed in the masked condition, and more broadly so in the unmasked condition.

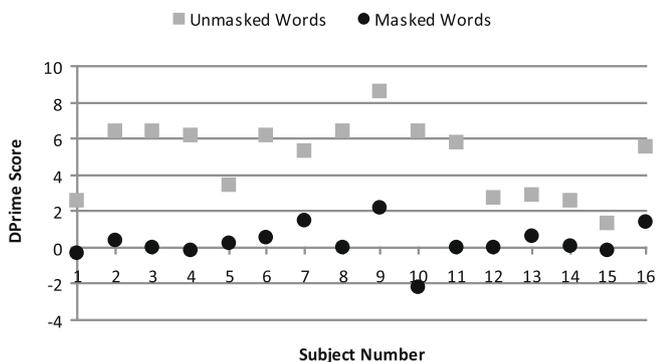


Fig. 3. Subjects' discrimination performance to detect the repetition of unmasked and masked target words. Scores deviated significantly from zero in response to unmasked trials only, confirming subliminal perception of masked words.

category labels as primes, and exemplars and non-exemplars as masked targets, Stenberg et al. (2000) compared the N400 priming effect for targets participants could consciously identify with those they could not, using a variety of methods to assess conscious identification (verbal report, six-alternative forced choice, and binary categorization). Consistent with our finding that unmasked targets yielded larger and more broadly distributed priming effects than masked, Stenberg et al. report larger and more broadly distributed N400 priming effects for stimuli participants could report than for those they could not. However, small N400 priming effects were observed for masked targets that were not identified. Similarly, in the present study, small N400 contextual congruency effects were observed for masked target words.

In addition to the N400 effects, sentence context also impacted the amplitude of the P2 component in the ERPs measured 200–

300 ms after word onset as P2 amplitude was enhanced in congruous relative to incongruous contexts. Congruity effects on the P2, moreover, were similar for masked and unmasked words, suggesting the processing mechanisms underlying the P2 are not dependent on conscious access. The observed P2 effect was an unexpected finding, given that P2 effects have not previously been observed with the present stimulus set in prior work in our laboratory (Brang et al., 2008, in press). However, P2 enhancement in congruous sentence contexts has previously been reported, and attributed to the detection of complex visual features involved in reading (Coulson et al., 2005; Federmeier, Wlotko, De Ochoa-De-wald, & Kutas, 2007). Our observation here of the influence of predictive sentence context on visual word form processing is in keeping with recent reports of an early influence of context on brain regions mediating the visual processing of faces (Cox, Meyers, & Sinha, 2004; Meeren, van Heijnsbergen, & de Gelder, 2005) and objects in scenes (Bar et al., 2006). The impact of sentence context on the brain response to masked words is also consistent with reports that masked faces result in differential amygdala activation as a function of emotional expression (Whalen et al., 1998) and prior fear conditioning (Morris, Öhman, & Dolan, 1998). Just as the visual processing of scenes and faces has been shown to benefit from statistical regularities in the concurrent context, these data suggest the visual processing of words is affected by linguistically evoked context information.

Whereas previous investigators have reported the influence of one-word contexts on the unconscious processing of words, the present study is the first to demonstrate the impact of sentence context on the processing of words not available for conscious report. These findings are, however, tempered by two caveats. The first concerns the presence of lexical associates in the sentence primes. Although sentence contexts were matched for the presence of known lexical associates preceding congruous and incongruous

target words, and it is unlikely that associative links between congruous targets and their contexts were stronger than those between incongruous targets and their sentence contexts, it is impossible to completely rule out this possibility. The second caveat is that the small contextual priming effect observed for masked words could reflect a small number of trials in which participants consciously registered the identity of masked words. This possibility is, however, undermined by our failure to observe a relationship between the size of our participants' N400 masked congruity effect and their performance on the discrimination task.

However, to further address this possibility, we used grand average ERPs to unmasked stimuli to simulate the way in which the inclusion of consciously processed stimuli could impact ERPs to masked stimuli. For example, if we assume that a participant was able to consciously identify 1/80 masked stimuli, we simulated an ERP to congruous sentence completions by averaging 1 unmasked congruous waveform with 79 masked congruous waveforms; to simulate an ERP to incongruous sentence completions we averaged 1 unmasked incongruous waveform with 79 masked congruous waveforms. These simulations indicated that the conscious identification of more than 18/80 trials would be necessary to yield the 0.6 microvolt sentence congruity effect observed in the present study. This rate of identification is highly unlikely in view of participants' chance-level performance on the discriminability task.

Taken at face value, however, these data indicate that congruity with the sentence context affected the brain response to masked words that were not consciously identified. This suggests automatic priming mechanisms need not depend on word-level associations, but can incorporate aspects of semantic and pragmatic context. Rather than positing links between sentence fragments and lexical (word) representations, however, contextual priming might be mediated by the activation of frames or schemas (Foss, 1982). For example, "When she grew up she wanted to be a" might activate a schema for 'female professions' which in turn might pre-activate a number of associated word representations such as "teacher" or "nurse". This explanation of context effects in language comprehension is in keeping with an important role for fast, passive memory retrieval processes in computational models of text processing (McKoon & Ratcliff, 1998), and shares important aspects with the proposal that the early activation of context frames provides top-down guidance of cortical object recognition processes (Bar, 2004).

Results of the present study also point to a possible connection between the neural substrate of the N400 and the system of conceptual short-term memory (Potter, Moryadas, Abrams, & Noel, 1993; Potter, 1999). As for sensory stores such as iconic (Sperling, 1960) and echoic (Crowder & Morton, 1969) memory, conceptual short-term memory (CSTM) is thought to be a high capacity system with rapid forgetting. Unlike sensory stores, however, information in CSTM is processed to the point of identification. CSTM is part of a two-staged model of visual processing involving preconscious processing in CSTM, followed by the slow, capacity-limited consolidation in working memory that is needed for conscious report (Chun & Potter, 1995).

Support for this proposal can be found in the attentional blink paradigm, that is, visual target identification tasks in which healthy adults are asked to detect two different targets in a stream of distractor stimuli presented at rates of 10–12 Hz. The attentional blink refers to the period between 200 and 500 ms after the presentation of the first target (T1), during which detection rates for the second target (T2) fall precipitously due to engagement of capacity-limited attentional processes in the detection of T1. Once T1 has been consolidated, the attentional system is again available for T2 processing; thus target detection rates improve when T2 is presented more than 500 ms after T1 (Shapiro, Arnell, & Raymond, 1997).

The neural substrate of CSTM has been studied with functional magnetic resonance imaging (fMRI) during the attentional blink paradigm in which targets were faces (T1) and place scenes (T2) (Marois, Yi, & Chun, 2004). T2 targets participants were unable to consciously identify nonetheless activated the parahippocampal place area (PPA), suggesting that unconsciously processed information is subjected to high-level visual processing in the ventral pathway (Marois et al., 2004). Enhanced PPA activity was found for consciously detected T2 targets, along with lateral frontal activations in both hemispheres (Marois et al., 2004). These findings suggest that the neural substrate of CSTM is the occipito-temporal areas in the ventral visual stream, whereas activity in lateral frontal cortex is critical for conscious target report.

Potter (1993) proposes that both language comprehension and scene perception involve the fleeting activation of conceptual information which in turn leads to the retrieval of additional information from long-term memory. Information that can be organized into a meaningful structure is consolidated, and stored in long-term memory; nonstructured material is forgotten. Importantly, CSTM is not a passive store, but rather a dynamic process in which novel connections can be established between activated conceptual structures. The generative capacity of CSTM may be one aspect of our ability to comprehend novel scenes as well as novel sentences.

A connection between the language comprehension processes indexed by the N400 effect and CSTM is consistent with a shared neural substrate in the left temporal lobe. In an integrative review, Lau et al. (2008) argue that fMRI studies support the contribution of the left posterior middle temporal gyrus to N400 priming effects, and, for spoken words, accompanying activity in the (left) superior temporal sulcus and gyrus. Magnetoencephalography (MEG) using distributed source estimates suggest activity 250–500 ms is generated in the (left hemisphere) planum temporale, middle temporal gyrus, and inferior temporal cortex, with later activity in left anterior temporal and inferior frontal cortex as well as right orbital and anterior temporal cortex (Halgren et al., 2002). Intra-cranial recordings in epileptic patients also suggest additional N400 generators in the anterior medial temporal lobe (McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995), a brain region whose activity is difficult to register with MEG, but is readily evident in the EEG.

Indeed, Van Petten and Luka (2006) argue that a large portion of the left temporal lobe participates in the generation of the N400 effect, along with some activity in the right temporal lobe. These researchers suggest the N400 component indexes the difficulty of retrieving associated information in semantic memory based both on representation of word meaning, and contextually activated retrieval cues. Moreover, the N400 has been shown to be sensitive to lexical priming when either the prime (Rolke, Heil, Streb, & Henninghausen, 2001) or the target (Luck, Vogel, & Shapiro, 1996) word was presented during the attentional blink.

Our demonstration of N400 sentence congruity effects for unconsciously processed words is consistent with the generative capacity of CSTM, and may indicate that priming results not from the passive spread of activation in a network, but rather from an active integrative process mediated by conceptual information (O'Connor & Potter, 2002; Ratcliff & McKoon, 1988). However, further research is needed to determine the generality of these results, and whether different sorts of conceptual information can impact conscious versus unconscious processing of words.

References

- Allopena, P. D., Magnuson, J. S., & Tanenhaus, M. K. (1998). Tracking the time course of spoken word recognition using eye movements: Evidence for continuous mapping models. *Journal of Memory and Language*, 38, 419–439.

- Anderson, J. E., & Holcomb, P. J. (1995). Auditory and visual semantic priming using different stimulus onset asynchronies: An event-related brain potential study. *Psychophysiology*, 32(2), 177–190.
- Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, 5(8), 617–629.
- Bar, M., Kassar, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences*, 103(2), 449–454.
- Bentin, S., McCarthy, G., & Wood, C. C. (1985). Event-related potentials, lexical decision and semantic priming. *Electroencephalography and Clinical Neurophysiology*, 60(4), 343–355.
- Besson, M., Fischler, I., Boaz, T., & Raney, G. (1992). Effects of automatic associative activation on explicit and implicit memory tests. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 18(1), 89–105.
- Besson, M., Kutas, M., & Petten, C. V. (1992). An event-related potential (ERP) analysis of semantic congruity and repetition effects in sentences. *Journal of Cognitive Neuroscience*, 4(2), 132–149.
- Boddy, J. (1986). Event-related potentials in chronometric analysis of primed word recognition with different stimulus onset asynchronies. *Psychophysiology*, 23(2), 232–245.
- Brang, D., Edwards, L., Ramchandran, V. S., & Coulson, S. (2008). Is the sky 2? Contextual priming in grapheme-color synaesthesia. *Psychological Science*, 19, 421–428.
- Brang, D., Kanai, S., Ramchandran, V. S., & Coulson, S. (in press). Contextual priming in grapheme-color synesthetes and yoked controls: 400 milliseconds in the life of a synesthete. *Journal of Cognitive Neuroscience*.
- Brown, C., & Hagoort, P. (1993). The processing nature of the N400: Evidence from masked priming. *Journal of Cognitive Neuroscience*, 5(1), 34–44.
- Brown, C. M., Hagoort, P., & Kutas, M. (2000). Postlexical integration processes in language comprehension: Evidence from brain-imaging research. *The New Cognitive Neurosciences*, 881–895.
- Chun, M. M., & Potter, M. C. (1995). A two-stage model for multiple target detection in rapid serial visual presentation. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 109–127.
- Chwilla, D. J., Brown, C. M., & Hagoort, P. (1995). The N400 as a function of the level of processing. *Psychophysiology*, 32(3), 274–285.
- Coulson, S., Federmeier, K. D., Petten, C. V., & Kutas, M. (2005). Right hemisphere sensitivity to word- and sentence-level context: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 31(1), 129–147.
- Cox, D., Meyers, E., & Sinha, P. (2004). Contextually evoked object-specific responses in human visual cortex. *Science*, 304(5667), 115–117.
- Crowder, R. G., & Morton, J. (1969). Precategorical acoustic storage (PAS). *Perception and Psychophysics*, 5(6), 365–373.
- Deacon, D., Hewitt, S., Yang, C. M., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: Evidence that the N400 does not reflect a post-lexical process. *Cognitive Brain Research*, 9(2), 137–146.
- Dehaene, S., Naccache, L., Le Clec'h, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. (1998). Imaging unconscious semantic priming. *Nature*, 395(6702), 597–599.
- DeLong, K. A., Urbach, T. P., & Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience*, 8(8), 1117–1121.
- Elman, J., & McClelland, J. (1986). The TRACE model of speech perception. *Cognitive Psychology*, 18(2), 1–86.
- Federmeier, K. D., Wlotko, E. W., De Ochoa-Dewald, E., & Kutas, M. (2007). Multiple effects of sentential constraint on word processing. *Brain Research*, 1146, 75–84.
- Forster, K. I. (1976). *Accessing the mental lexicon. New approaches to language mechanisms: A collection of psycholinguistic studies* (pp. 257–287).
- Forster, K. I. (1981). Priming and the effects of sentence and lexical contexts on naming time: Evidence for autonomous lexical processing. *The Quarterly Journal of Experimental Psychology Section A*, 33(4), 465–495.
- Forster, K. I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 10(4), 680–698.
- Foss, D. J. (1982). A discourse on semantic priming. *Cognitive Psychology*, 14(4), 590–607.
- Gaskell, G., & Marslen-Wilson, W. (1997). Integrating form and meaning: A distributed model of speech perception. *Language and Cognitive Processes*, 12(5/6), 613–656.
- Grainger, J., & Jacobs, A. M. (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological Review*, 103, 518–565.
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24(2), 95–112.
- Halgren, E. et al. (2002). N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *Neuroimage*, 17, 1101–1116.
- Holcomb, P. J. (1988). Automatic and attentional processing: An event-related brain potential analysis of semantic priming. *Brain and Language*, 35(1), 66–85.
- Holcomb, P. J., Reder, L., Misra, M., & Grainger, J. (2005). The effects of prime visibility on ERP measures of masked priming. *Cognitive Brain Research*, 24(1), 155–172.
- Kiefer, M. (2002). The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Cognitive Brain Research*, 13(1), 27–39.
- Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, 4(12), 463–470.
- Kutas, M., Federmeier, K. D., Staab, J., & Klueder, R. (2007). Language. In J. Cacioppo, L. Tassinari, & G. Berntson (Eds.), *Handbook of psychophysiology* (pp. 555–580). Cambridge: Cambridge University Press.
- Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, 207(4427), 203.
- Kutas, M., & Hillyard, S. A. (1989). An electrophysiological probe of incidental semantic association. *Journal of Cognitive Neuroscience*, 1(1), 38–49.
- Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (De)constructing the N400. *Nature Reviews Neuroscience*, 9(12), 920–933.
- Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature*, 383, 616–617.
- Marois, R., Yi, D.-J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron*, 41, 465–472.
- McCarthy, G., Nobre, A. C., Bentin, S., & Spencer, D. D. (1995). Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *Journal of Neuroscience*, 15, 1080–1089.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: Part I. An account of basic findings. *Psychological Review*, 88, 375–407.
- McKoon, G., & Ratcliff, R. (1998). Memory-based language processing: Psycholinguistic research in the 1990s. *Annual Review of Psychology*, 49(1), 25–42.
- Meeren, H. K. M., van Heijnsbergen, C. C. R. J., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences*, 102(45), 16518–16523.
- Misra, M., & Holcomb, P. J. (2003). Event-related potential indices of masked repetition priming. *Psychophysiology*, 40(1), 115–130.
- Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393(6684), 467–470.
- Neely, J. H. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. *Basic Processes in Reading: Visual Word Recognition*, 11.
- Nobre, A. C., & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. *Journal of Neuroscience*, 15, 1090–1098.
- O'Connor, K. J., & Potter, M. C. (2002). Constrained formation of object representations. *Psychological Science*, 13(2), 106–111.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Posner, M., & Snyder, C. (1975). Facilitation and inhibition in the processing of signals. *Attention and Performance V*, 669–682.
- Potter, M. C. (1993). Very short-term conceptual memory. *Memory & Cognition*, 21, 156–161.
- Potter, M. C. (1999). Understanding sentences and scenes: The role of conceptual short-term memory. *Fleeting Memories: Cognition of Brief Visual Stimuli*, 13–46.
- Potter, M. C., Moryadas, A., Abrams, I., & Noel, A. (1993). Word perception and misperception in context. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 19, 3–22.
- Ratcliff, R., & McKoon, G. (1988). A retrieval theory of priming in memory. *Psychological Review*, 95(3), 385–408.
- Rolke, B., Heil, M., Streb, J., & Henninghausen, E. (2001). Missed target words within the attentional blink evoke an N400 semantic priming effect. *Psychophysiology*, 38(2), 165–174.
- Rugg, M. D. (1985). The effects of semantic priming and word repetition on event-related potentials. *Psychophysiology*, 22(6), 642–647.
- Schnyer, D. M., Allen, J. J. B., & Forster, K. I. (1997). Event-related brain potential examination of implicit memory processes: Masked and unmasked repetition priming. *Neuropsychology*, 11, 243–260.
- Shapiro, K. L., Arnell, K. M., & Raymond, J. E. (1997). The attentional blink. *Trends in Cognitive Science*, 1, 291–296.
- Smith, M. E., & Halgren, E. (1989). Dissociation of recognition memory components following temporal lobe lesions. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 15(1), 50–60.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs*, 74, 1–29.
- Stenberg, G., Lindgren, M., Johansson, M., Olsson, A., & Rosen, I. (2000). Semantic processing without conscious identification: Evidence from event-related potentials. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 26(4), 973–1004.
- Taft, M. (1994). *Reading and the mental lexicon*. Psychology Press.
- Traxler, M. J. (2000). Priming in sentence processing: Intralexical spreading activation, schemas, and situation models. *Journal of Psycholinguistic Research*, 29(6), 581.
- Van Petten, C., & Luka, B. J. (2006). Neural localization of semantic context effects in electromagnetic and hemodynamic studies. *Brain and Language*, 97, 279–293.
- Whalen, P. J., Rauch, S. L., Etkoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, 18(1), 411–418.
- Wlotko, Edward W., & Federmeier, Kara D. (2007). Finding the right word: Hemispheric asymmetries in the use of sentence context information. *Neuropsychologia*, 45(13), 3001–3014.
- Wu, Y. C., & Coulson, S. (2005). Meaningful gestures: Electrophysiological indices of iconic gesture comprehension. *Psychophysiology*, 42(6), 654–667.