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Short Communication

Before the N400: Effects of lexical–semantic violations in visual cortex

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ABSTRACT

There exists an increasing body of research demonstrating that language processing is aided by context-based predictions. Recent findings suggest that the brain generates estimates about the likely physical appearance of upcoming words based on syntactic predictions: words that do not physically look like the expected syntactic category show increased amplitudes in the visual M100 component, the first salient MEG response to visual stimulation. This research asks whether violations of predictions based on lexical–semantic information might similarly generate early visual effects. In a picture–noun matching task, we found early visual effects for words that did not accurately describe the preceding pictures. These results demonstrate that, just like syntactic predictions, lexical–semantic predictions can affect early visual processing around ~100 ms, suggesting that the M100 response is not exclusively tuned to recognizing visual features relevant to syntactic category analysis. Rather, the brain might generate predictions about upcoming visual input whenever it can. However, visual effects of lexical–semantic violations only occurred when a single lexical item could be predicted. We argue that this may be due to the fact that in natural language processing, there is typically no straightforward mapping between lexical–semantic fields (e.g., flowers) and visual or auditory forms (e.g., *tulip*, *rose*, *magnolia*). For syntactic categories, in contrast, certain form features do reliably correlate with category membership. This difference may, in part, explain why certain syntactic effects typically occur much earlier than lexical–semantic effects.

1. Introduction

A relatively consistent finding in electrophysiological studies of language processing is that certain syntactic factors affect neural processing at an earlier time-point than lexical–semantic violations do: while event-related potentials to word category violations are sometimes observed as early as ~125 ms after the onset of an unexpected word (e.g., Friederici, Pfeifer, & Hahne, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991), neural correlates of lexical–semantic factors and world knowledge are typically indexed by a sustained negative-going wave peaking around 400 ms (the N400 component; e.g., Kutas, Van Petten, & Kluender, 2006). Some scholars have taken this as evidence in favor of an account where syntactic properties of words are accessed first (in left-anterior and left-temporal cortex), only after which lexical–semantic features are analyzed (e.g., Friederici, 2002). However, such a strictly modular and bottom-up view of language processing is challenged by recent evidence pertaining to the localization of early word category effects, as well as by the increasing body of research demonstrating the importance of context-based predictions in explaining neural effects of language processing.

Dikker, Rabagliati, and Pylkkänen (2009) and Dikker, Rabagliati, Farmer, and Pylkkänen (2010), for instance, report a series of results showing that responses to word category violations localize to sensory cortex. Using magnetoencephalography (MEG), the authors found that the visual M100 component, the first salient response to visual stimulation generated in visual cortex around 100 ms post-stimulus onset, was sensitive to the probabilistic distribution of form features across syntactic categories (based on a phonological typicality measure conducted over English nouns and verbs by Farmer, Christiansen, and Monaghan (2006). For example, in cases where a verbal form was predicted (e.g., *the beautifully* __, predicting for the participle form of a verb), the amplitude of the M100 component in response to a noun like *prince* depended on the 'nouniness' of *prince*: higher M100 amplitude was found for nouns with form features that are not shared with many verbs. Because previous studies strongly suggest that the visual M100 is a pre-lexical, low-level visual response (e.g., Solomyak & Marantz, 2009; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999), Dikker et al. argued that a strictly bottom-up interpretation of these findings is implausible. Instead of an account where word form processing, word category access, and syntactic structure building all occur within the time-frame of

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early sensory processing, Dikker et al. proposed the *Sensory Hypothesis*, according to which the brain generates estimates about the likely physical appearance of upcoming words based on syntactic predictions: words that do not 'look like' the expected syntactic category affect sensory processing.

A predictive account of such early sensory effects is in line with the increasing body of research demonstrating the role of predictive processing in language comprehension (e.g., Altmann & Kamide, 1999; McDonald & Shillock, 2003; Staub & Clifton, 2006; DeLong, Urbach, & Kutas, 2005; Federmeier, 2007; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005). For syntactic violations, for example, Lau, Stroud, Plesch, and Phillips (2006) found a greater early negativity (ELAN) to violations of strongly, as compared to weakly, predicted word categories, and some studies have shown that the amplitude of early ERPs to target words (in particular the P2 component) is affected by whether or not the sentential context is highly predictive (e.g., Wlotko & Federmeier, 2007). Similarly, latency and amplitude variations of the N400 component seem to be best explained in terms of facilitation of lexical access by way of contextual prediction or lexical priming (e.g., Federmeier & Kutas, 1999; Lau, Almeida, Hines, & Poeppel, 2009).

The observation that sensory cortices are sensitive to word category violations, a finding that was recently replicated for the auditory modality by Herrmann, Maess, Hasting, and Friederici (2009), may contribute to elucidating why syntactically relevant responses occur so early. However, accepting that previously generated predictions affect processing does not in itself explain the empirical generalization that syntactic effects take place before lexical–semantic effects.

One possibility is that syntactic prediction and lexical–semantic prediction constitute qualitatively different processes: maybe syntactic prediction involves the top-down activation of form representations, whereas lexical–semantic prediction does not. However, previous studies suggest that lexical–semantic prediction does in fact include the preactivation of word form properties. For example, Laszlo and Federmeier (2009) show that orthographic similarity to predicted words affects N400 amplitude. Similar experiments in the auditory domain have demonstrated that words that violate phonological, but not semantic, predictions generate an ERP effect that can be dissociated from the N400 response (the phonological mismatch negativity; see e.g., Connolly & Phillips, 1994). In addition, a recent MEG study using a cross-modal sentence–picture priming task found that the M100 response was sensitive to whether or not a picture matched the scene described in an auditorily presented sentence (Hirschfeld, Zwitserlood, & Dobel, 2010). This result suggests that predictions based on semantic properties can affect early visual processing, possibly via the same mechanisms as syntactic prediction. In Hirschfeld et al.'s study, the sentences described unambiguous scenes, thus allowing for quite specific predictions regarding the upcoming visual scene. In natural language processing, however, generating form-estimates based on lexical–semantic predictions may not always be possible. Whereas syntactic category maps onto certain form properties (form typicality; Farmer et al., 2006, see above), no such straightforward form correlate exists for lexical–semantic fields (with exceptions such as *boil/broil*). For example, while *rose* and *magnolia* are semantically related but unrelated in form, *rose* and *hose* show form, but not meaning similarity. As a result, lexical–semantic predictions might be translated into form-based estimates only when there is either a single lexical element predicted (a guaranteed one-to-one mapping between meaning and form) or when form features are sufficiently shared between multiple candidates. In the majority of studies investigating lexical–semantic processing, however, context does not set up a prediction for one particular word for all items in the experiment, and for those cases where a limited set of words can be predicted, these may not be sufficiently related in form. Similarly, while factors like bigram frequency and orthographic and phonological neighborhood density are typically taken into account in studies that investigate lexical–semantic processing, it is not usually asked if the violating word is sufficiently distinct from the predicted word(s) in terms of form features. The results of Dikker et al. (2010) suggest that such form distinctiveness is necessary for early visual effects to arise: possibly, higher M100 amplitude to unpredicted items reflects the processing cost associated with reactivating suppressed form representations contained in unexpected words.

An additional possible reason as to why early visual effects of violations of lexical–semantic predictions have not been found before is methodological in nature: most studies investigating lexical–semantic violations have used EEG, for which analyses are usually performed over averages across relatively large time-intervals. While such analyses are appropriate for sustained components such as the N400, sensory responses like the M100 do not constitute long-lasting activity, and thus a peak-focused analysis of amplitude variation as a function of predictability is more appropriate.

To investigate whether early sensory responses such as the M100 component can be sensitive to violations of lexical–semantic predictions, we employed a task where participants were asked whether a noun phrase accurately described the preceding picture, as such ensuring a straightforward and unambiguous mapping between meaning and form. Pictures of 80 different objects were used to set up specific expectations for just one lexical item in the subsequent noun phrase (e.g., a picture of an apple priming the word *apple*) and participants knew beforehand which word was the appropriate match. In the case of a violation of a prediction, the target word's form was manipulated such that it was maximally distinct from the predicted word's form. An additional match/mismatch comparison was included where no specific prediction for a particular word form could be generated based on the preceding picture. Instead, pictures presented in these conditions represented an entire semantic field (a picture of a grocery bag stood for any word describing an edible or drinkable object, and a picture of Noah's Ark for any noun describing an animal). Thus, we varied both the nature of the picture prime (Context: +Predictive vs. −Predictive), and whether or not the noun phrase matched the preceding picture (congruence: Match vs. Mismatch). In contrast to the +Predictive trials, no early visual effects of congruence were expected within the −Predictive trials, as no specific form-estimates could be generated based on a prediction for any word pertaining to a semantic field. The design is presented in Table 1.

It has been shown that intermixing experimental conditions for which task-strategies are potentially different may negatively interfere with processing (see e.g., Monsell, 2003 for review). Therefore, to avoid effects of interests from being masked as a result of task-related factors, non-predictive trial types were only intermixed with predictive trials during the second half of the experiment (hereafter referred to as Block 2).

In addition to early visual effects, we expected effects of congruence in the N400 time-window, consistent with a large body of extant research on lexical–semantic processing. Specifically, we expected congruence to affect amplitude of the M350 component, a subcomponent of the N400 m response as measured in MEG, which has been associated with lexical access (e.g., Pylkkänen & Marantz, 2003).

In sum, the primary goal of this experiment was to establish whether violations of lexical–semantic predictions can affect early sensory processing, just like violations of syntactic predictions. Such a finding would strongly challenge a strict bottom-up view of language processing and would support models where contextual predictions facilitate top-down effects on low-level sensory regions.

Table 1
Examples of experimental stimuli.

+ / - PRED	PICTURE (900 ms)	NOUN PHRASE (300 ms on/off)	+ / - MATCH	# of items
+ prediction for specific word (form)		+ the apple	+ MATCH	BLOCK 1: 80 BLOCK 2: 80
		+ the apple	- MATCH	BLOCK 1: 80 BLOCK 2: 80
- prediction for specific word (form)	 [any food/drink item]	+ the apple	+ MATCH	BLOCK 2: 80
	 [any animal]	+ the apple	- MATCH	BLOCK 2: 80

* BLOCK 1: only + PRED conditions (80 x match / 80 x mismatch)
* BLOCK 2: + PRED conditions intermixed with - PRED conditions

Examples of experimental stimuli of (80 per condition; 40 animals and 40 food/drink items). +Predictive conditions were presented twice: once in isolation (Block 1) and once intermixed with −Predictive conditions (Block 2).

2. Results

Fig. 1 displays waveforms for sensors of interest (see Section 4.5 for details) at the M100 peak (A and B) and over left-hemisphere sensors (C) for both predictive (1.1) and non-predictive (1.2) comparisons.

2.1. The M100 response

A 2 (Congruence: Match vs. Mismatch) by 2 (Block: Block 1 vs. Block 2) within-subjects ANOVA over Predictive trials revealed a main effect of Congruence on the M100 response ($F(1, 14) = 11.444$, $p = .004$): higher M100 amplitude was found for Mismatch trials as compared to Match trials (see Fig. 1.1A and B; peak activity from left and right hemisphere sensors were combined for analysis, see Section 4.5). There was no main effect of Block ($F(1, 14) = .067$, $p = .799$) nor an interaction between Congruence and Block ($F(1, 14) = .351$, $p = .351$), suggesting that there was an effect of congruence on the M100 response for predictive trials across the entire experiment, and that this effect did not differ reliably depending on either presentation order or on intermixing of trial types. In contrast to the +Predictive comparison, there was no effect of Congruence on the M100 component when comparing Match vs. Mismatch trials for –Predictive trials ($t(14) = .046$, $p = .96$; Fig. 1.2A and B; peak activity from left and right hemisphere sensors were combined for analysis, see Section 4.5). This result corroborates the hypothesis that the visual M100 component is sensitive to whether a word matches a lexical–semantic prediction but only if there is a straightforward form correlate of the lexical–semantic level (in the +Predictive manipulation, but not the −Predictive manipulation).

T-statistics over 10 ms intervals in the time-window preceding the M100 response (between 0 and 100 ms) revealed no reliable differences in any of the comparisons.

2.2. 250–400 ms time window, left-hemisphere sensors

Analyses over sensor data extracted from the left-hemisphere (Fig. 1.1.C and 1.2.C), averaged from 250 to 400 ms revealed a similar pattern of results as for the M100 response: a main effect of Congruence ($F(1, 14) = 19.833$, $p < .001$) and no main effect of Block ($F(1, 14) = .085$, $p = .775$) or interaction between Congruence and Block ($F(1, 14) = 2.492$, $p = .137$) in the 2 (Congruence: Match vs. Mismatch) by 2 (Block: Block 1 vs. Block 2) within-subjects ANOVA over Predictive trials (Fig. 1.1.C), and no effect of Congruence for the non-Predictive comparison ($t(14) = .276$, $p = .787$; Fig. 1.2.C). Thus, effects in the 250–400 ms time-window surfaced for predictive contexts only, just like for the M100 component. As can be seen when comparing Fig. 1.1.C and 1.2.C, there was less activity for the +Predictive/+Match trials compared to all other conditions (+Predictive/+Match: Mean = −1.33 fT; −Predictive/+Match: Mean = −9.16 fT;+Predictive/-Match: Mean = −7.69 fT; −Predictive/−Match: Mean = −9.19 fT).

3. Discussion

The goal of the current work was to contribute to our understanding of predictive processing in language comprehension. It has been proposed that the brain continuously generates predictions about upcoming events (Bar, 2007). These predictions then affect processing of incoming stimuli. In some cases, expectations can be translated into estimates about the visual or auditory form of the anticipated input. The brain may then derive expectations about the auditory or visual properties via top-down modulation from higher cortex to lower-level sensory areas (e.g., Summerfield & Koechlin, 2008). Such predictive top-down processing subsequently affects sensory processing of incoming stimuli.

As summarized above, in Dikker et al. (2010) we studied syntactic prediction, and found results that are compatible with such a top-down explanation of how syntactically relevant factors can affect neural responses as early as 100 ms after word presentation: in reading, words whose form was not typical for the expected word category generated more activity in visual cortex than words whose form properties did map onto the word category expectations. Here, we investigated whether the brain also generates form-estimates based on lexical–semantic prediction, and found that, indeed, the visual M100 component, an early sensory response measured in MEG, showed higher amplitudes to words that violated predictions for lexical items as compared to words that satisfied a prediction. These data suggest that the brain generates form-estimates not only in syntactic processing, but also in lexical–semantic prediction.

As pointed out in the Introduction, one possible explanation for why early sensory effects are typically only found for violations of syntactic predictions is that generating estimates about visual forms based on lexical–semantic predictions may not very often be possible or helpful in everyday communicative contexts: in contrast to syntax, where word form features correlate with word category, there exists no straightforward mapping between semantic relatedness and form relatedness.

How such differences may affect early sensory processing of lexical–semantic vs. syntactic violations can be understood in light of a model where the preactivation of predicted form representations involves a combination of activating expected form features in sensory cortex and simultaneously suppressing irrelevant ones. Such an approach to form-prediction is consistent with biased competition models of visual attention (e.g., Desimone & Duncan, 1995) and predictive coding models (e.g., Friston, 2005). When a form-prediction is violated, suppressed representations need to be reactivated, and it may be this change in activation that is measured as increased M100 amplitude. Given that predictions for syntactic categories such as nouns and verbs are generated at a very high rate, features pertaining to a specific syntactic category are probably very often co-activated, and syntactically relevant form representations may even be represented as clusters in sensory cortex. This may allow for an efficient top-down biasing process

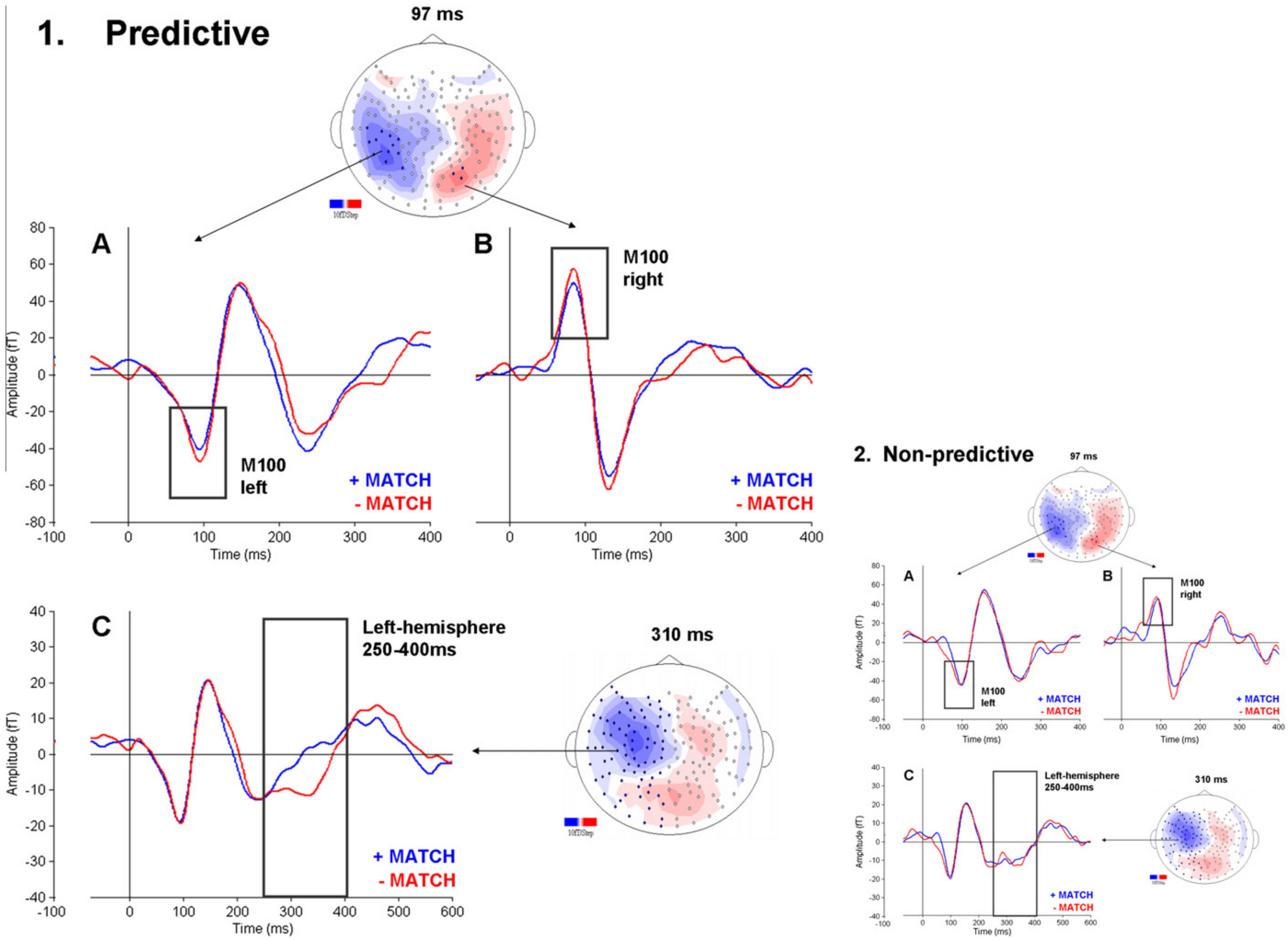

Fig. 1. Sensor waveforms per condition. Grandaveraged waveforms per comparison for M100 (A and B) and left-hemisphere (C) sensors of interest per comparison ($n = 15$; blue: match; red: mismatch. Top views of field patterns (for grandaveraged data) for each component (blue: re-entering field, red: outgoing field), and sensors of interest (color filled sensors) are plotted. Note that for the M100 peak, all statistics were performed over activity from left and right hemisphere sensors combined.

by which clusters of neuronal populations are excited and others are suppressed. For lexical–semantics, this is less obviously the case: apart from isolated cases such as *broil*/*boil*, it is unclear that there exist clusters of form-features corresponding to, say, the semantic category "flower", that can be isolated from "animal" form features in the same way that "noun" and "verb" can. As a result, when an unpredicted lexical item is encountered, changes in activation associated with reactivating suppressed form representations may be either non-existent or too small-scale to be detectable with current non-invasive neuroimaging techniques. It is important to emphasize, however, that the present study merely shows that early visual effects of lexical–semantic violations *can* be observed under conditions where there exists a mapping between lexical–semantics and form. We cannot rule out, for example, that the absence of any previous reports of similar findings was the result of differences in analysis procedures between those studies and ours (e.g., analyzing data averaged across large time-intervals vs. a focused analysis on peak amplitude). Future research should investigate the exact conditions under which early sensory effects of lexical–semantic prediction may or may not arise.

As was predicted based on previous studies investigating lexical–semantic violations, we also saw an effect of congruence in a later time-window, and across the entire experiment: less activity was found for nouns that matched specific predictions as compared to the other three conditions. This pattern of results, especially the fact that matching trials in non-predictive contexts showed the same amplitudes as mismatch trials in either predictive or non-predictive contexts, is compatible with an account whereby a picture prime triggers the preactivation of the lexical representation of a given noun, as a result of which less processing cost is incurred when this noun was actually presented (see e.g., Lau et al., 2009 for similar arguments). In non-predictive contexts, processing match and mismatch trials would be equally costly because participants could not benefit from lexical preactivation.

Recently, Hirschfeld, Zwitserlood, and Dobel (2010; see Introduction) also reported a combination of early and late effect. Comparing three types of pictures (matches, related mismatches and unrelated mismatches) they found that M100 amplitude was affected by congruency only (match vs. mismatch), while brain activity in the N400 time-window was also sensitive to relatedness. This corroborates the hypothesis that visual form predictions may only be generated if a single lexical entry is anticipated. It also supports a view whereby the M100 and M350 components represent different levels of analysis, with the former responding to physical properties, and the latter to lexical–semantic properties.

In sum, the results of this experiment demonstrate that the M100 response is not solely sensitive to form features associated with syntactic category, but can also be responsive to violations of form-expectations that are based on lexical–semantic predictions. Thus, it appears that syntax is not "special" during the earliest stages of analysis. Rather, these findings suggest that when possible, the brain associates linguistic expectations (whether syntactic or lexical–semantic) with form-estimates.

4. Methods

4.1. Participants

After the exclusion of 3 participants based on low signal-to-noise ratio in the MEG data, and 4 other participants because they did not show typical early visual brain responses, 15 right-handed participants with normal or corrected-to-normal vision were included for analysis (7 male; mean age: 27).

4.2. Materials

Eighty different nouns were presented in four conditions in a 2 (Context: +Predictive vs. –Predictive) by 2 (Congruence: Match vs. Mismatch) design. Noun phrases either followed a picture denoting a specific object (+Predictive) or they followed a picture representing a semantic field (−Predictive). Nouns either matched the image or they did not. Visual properties of any word presented in the Mismatch condition of the Predictive context were maximally distinct from those of the predicted word, in terms of Levenshtein edit-distance (the number of letters that need to be replaced, removed, or added to convert one word into another; e.g., Navarro, 2001) and word length (nouns were binned into 'short' [3–5 letters] and 'long' [5–8 letters] nouns). Further, letters occurring in word pairs were maximally distinct in form (e.g., for any matching word starting with an *n*, there was no mismatch counterpart starting with an *h*).

Both the baseline and the target words were perfectly balanced: each noun (40 nouns denoting animals and 40 nouns denoting food/drink items) appeared once in each condition, and input preceding the target noun was kept constant across conditions for 1500 ms (from the offset of the picture to the onset of the target noun) to make sure that possible distinct brain activity resulting from processing different pictures had subsided by the time the noun phrase was presented.

4.3. Procedure

During the experiment, participants lay in a dimly lit, magnetically shielded room. Stimuli were presented using PsyScope X, and projected onto a screen positioned approximately 50 cm from the participant's eyes. Pictures were presented on a 75% grey background. Words were presented in white in non-proportional Courier font (size 28) against a 75% grey background. Participants engaged in a simple match/mismatch task for the types of stimuli presented in Table 1. Each trial began with a picture (see Section 4.2), presented for 900 ms followed by a 300 ms blank screen, after which a fixation cross appeared and then the noun phrase (word-by-word, 300 ms on/off). A question mark followed the noun phrase, prompting participants to hit the MATCH button (left index finger) if the noun phrase accurately described the preceding picture, or the MISMATCH button (left middle finger) if the noun phrase did not match the preceding image. At button press, the question mark was replaced by a feedback screen. Appearance of the next trial was self-paced. The experiment was divided into two blocks. Block 1 consisted only of +Predictive trials (see Introduction; presented in random order; 160 trials total). Block 2 contained both +Predictive and –Predictive trials (intermixed in random order; 320 trials total). The +Predictive trials were an exact repetition of the trials that had been presented in Block 1 (but not in the same order). The experiment was preceded by training and practice. Participants were introduced to the task (30 practice trials total), and it was explained to them that a picture of a grocery bag functioned as a stand-in for "any food/drink item" and that a picture of Noah's Ark represented "any animal." Prior to the experiment, participants were familiarized with all picture primes and corresponding nouns.

4.4. Data acquisition

Neuromagnetic fields were recorded continuously with a whole-head, 157-channel axial gradiometer array at a sampling rate of 1000 Hz in a band between 0 and 200 Hz. A notch filter of 60 Hz was applied. The entire recording session lasted approximately 45 min.

4.5. Data analysis

4.5.1. Pre-processing

Prior to averaging, the MEG data were cleaned of artifacts (in BESA 5.1) and trials on which participants provided an incorrect judgment. On average, this resulted in the exclusion of 15% of the data per subject. Data were averaged by stimulus category over a 900 ms epoch with a 300 ms pre-stimulus interval, time-locked to the appearance of the target word. Prior to analysis, recordings were high and low-pass filtered at 1 and 40 Hz respectively, consistent with Dikker et al. (2009, 2010) as well as a body of prior MEG work on the M350 and other brain responses in the N400 time-window (e.g. Embick, Hackl, Schaeffer, Kelepir, & Marantz, 2001; Pylkkänen, Stringfellow, & Marantz, 2002; Pylkkänen & McElree, 2007).

4.5.2. Sensors of interest analysis

For the M100 component, sensors of interest were identified based on the field pattern at the time-point of the M100 peak (97 ms) for data averaged across all participants and conditions. From both the re-entering field (left-hemisphere; blue; Fig. 1.1.A) and the outgoing field (right-hemisphere; red; Fig. 1.1.B), only those sensors were selected that showed activity at a threshold of >40 fT from zero (3 sensors from the right hemisphere and 12 sensors from the left-hemisphere). Activity recorded at these sensors was extracted for each condition, subject, and hemisphere separately. A weighted average between hemispheres was then constructed, after resigning the re-entering field's sensor waveforms. Analyses were conducted over the average activity across a 10 ms interval of interest centered around each condition's average peak activity.

In addition, we conducted t-statistics over 10 ms time-intervals between 0 and 100 ms to investigate possible differences between conditions prior to the M100 peak (note that a peak-based comparison as used for the M100 window is only appropriate for targeted analysis of clearly identifiable brain response components). *P*-values were corrected for multiple comparisons using the Bonferroni–Holm correction (Holm, 1979).

With respect to the N400 time-window, grandaveraged data showed two sustained components, between ~250–400 ms and 400–600 ms respectively. It has been previously noted that the long-lasting N400 response probably reflects a complex of several sub-components (Pylkkänen & Marantz, 2003; Van den Brink, Brown, & Hagoort, 2001), and a recent MEG study by Lau et al. (2009) similarly reports two components with distinct field patterns within the N400 time-range. We here focus on the first component, peaking around 325 ms (likely corresponding to the M350 component; Pylkkänen & Marantz, 2003). Because this component was relatively sustained and with a slightly varying field pattern strongest over left-hemisphere sensors (see field pattern from an example time-point in Fig. 1.1/2.C), we analyzed activity extracted from all left-hemisphere sensors averaged from 250 ms to 400 ms.

All data (peak activity per condition for the M100 response and averaged activity over left-hemisphere sensors from 250–400 ms) were entered into a 2 by 2 within-subjects ANOVA (Congruence: Match vs. Mismatch × Block: Block 1 vs. Block 2) over + Predictive trials. 2-tailed paired-sample *t*-tests were performed to investigate possible effects of Congruence in non-predictive trials.

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