

Predicting language: MEG evidence for lexical preactivation



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ABSTRACT

It is widely assumed that prediction plays a substantial role in language processing. However, despite numerous studies demonstrating that contextual information facilitates both syntactic and lexical-semantic processing, there exists no direct evidence pertaining to the neural correlates of the prediction process itself. Using magnetoencephalography (MEG), this study found that brain activity was modulated by whether or not a specific noun could be predicted, given a picture prime. Specifically, *before* the noun was presented, predictive contexts triggered enhanced activation in left mid-temporal cortex (implicated in lexical access), ventro-medial prefrontal cortex (previously associated with top-down processing), and visual cortex (hypothesized to index the preactivation of predicted form features), successively. This finding suggests that predictive language processing recruits a top-down network where predicted words are activated at different levels of representation, from more 'abstract' lexical-semantic representations in temporal cortex, all the way down to visual word form features. The same brain regions that exhibited enhanced activation for predictive contexts before the onset of the noun showed effects of congruence during the target word. To our knowledge, this study is one of the first to directly investigate the anticipatory stage of predictive language processing.

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1. Introduction

When interacting with our environment, we constantly anticipate upcoming events without even thinking about it: we walk down a supermarket aisle expecting a register at the end, we expect a dog to bark and not meow, and we generate expectations about what another person might say or do. In other words, the brain is a 'proactive' organ (Bar, 2007), continuously generating predictions about upcoming events. The role of prediction in (neuro)cognition has recently received a lot of attention, and there now exist several relatively comprehensive accounts of the sources and underlying mechanisms of predictive processing (e.g., Bar, 2007; Bubic, von Cramon, & Schuboltz, 2010; Enns & Lleras, 2008). Some scholars have argued that predictive processing is vital to our survival, as drawing analogies between past and possible future events allows us to estimate e.g., whether people surrounding us in the subway pose a possible threat. Language being one of the primary modes of human interaction, it may thus hardly come as a surprise that numerous studies have suggested that prediction plays a significant role in facilitating rapid and efficient communication (e.g., Altmann & Kamide, 1999; Federmeier, 2007; Van

Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Wicha, Moreno, & Kutas, 2003). To our knowledge, however, in spite of both theoretical and experimental advances in this area of research, evidence pointing to the neural mechanisms underlying the anticipatory stages of language processing is so far lacking: what happens *before* a predicted or unpredicted linguistic element is encountered?

Previous studies have convincingly shown that anticipatory processing can drive ERP responses to linguistic incongruencies (DeLong, Urbach, & Kutas, 2005; Van Berkum et al., 2005; Wicha et al., 2003). This research supports a hypothesis whereby anticipatory language processing entails the preactivation of linguistic representations that are associated with the predicted lexical or syntactic element in question (following e.g., Bubic et al., 2010). For example, when hearing a sentence fragment like "Grass is . . .," a listener is likely to activate "green" in his/her mental lexicon even before the adjective is heard. Predictions can occur within and between any level of representation: the lexical entry "grass" can predict for "green," but prediction can also take place between representations at different levels that are linked to a single concept. The latter type has been extensively studied within the context of audio-visual integration (see e.g., Arnal, Wyart, & Giraud, 2011 and references therein). In this study, we investigated the prediction of visual word forms based on images of objects, i.e., between representations that are each associated with a single concept.

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If generating a prediction for a certain input entails the preactivation of relevant representations in brain areas where said representations are stored, we might expect increased activity in such regions due to the ‘pre-excitement’ of these representations in order to facilitate subsequent processing. Such a hypothesis is in line with Sharpening Models of priming (Grill-Spector, Henson, & Martin, 2006) as well as biased competition models of attention (e.g., Desimone & Duncan, 1995).

Most evidence for expectation-based processing comes from studies that show increased activity in brain regions responsible for processing relevant types of sensory information. For example, gustatory cortices are activated in anticipation of food items (Simmons & et al., 2005), and somatosensory cortex is activated before somatosensory stimuli are presented (Carlsson & et al., 2000). Further, some promising findings are emerging from the literature on mental imagery: Results from Stokes, Thompson, Cusack, and Duncan (2009) suggest that visual imagery activates similar neural representations as those that are active in response to the actual visual presentation of an imagined shape, and similar findings have recently been reported for the auditory domain (Tian & Poeppel, 2010).

Importantly, however, this set of results only speaks to predictive processing indirectly: it remains to be investigated whether predictive processing and mental imagery recruit the same mechanisms, and the preactivation findings discussed above only show that excitement of certain brain areas correlates with the nature of a particular *type* of upcoming percept (if a person is in ‘eating mode,’ gustatory cortices are excited, if s/he is in ‘face mode,’ fusiform gyrus is probed (Summerfield & et al., 2006). Crucially, with the exception of multi-sensory integration (e.g., Arnal et al., 2011 and references therein), this prior research does not speak to the preactivation of representations of specific percepts (e.g., an Asian face, or the taste of a cupcake) and/or the possible suppression of irrelevant ones (e.g., a redhead; the burning sensation of red chili peppers when rubbed into one’s eye). A similar argument can be made for language processing: In reading, it is likely that attention is directed toward visual stimulation as opposed to auditory stimulation, with the corresponding neural consequences thereof, but this does not automatically entail that specific representations of upcoming visual word forms are preactivated.

The most direct evidence for the role of prediction in language processing comes from eye-tracking studies (Altmann & Kamide, 1999; Altmann & Mirkovic, 2009), as well as ERP research showing mismatch effects on words preceding a predicted noun, such as prenominal adjectives or determiners that are inconsistent with the gender or phonological properties of the expected noun (DeLong et al., 2005; Van Berkum et al., 2005; Wicha et al., 2003). Such effects, however, are likely to index expectancy violations rather than the preactivation process itself: Gender and phonotactics can be predicted along with a noun, and a mismatch in these features on e.g., a pronominal determiner would then be a violation of such a prediction. In this study, in contrast, we compare cases where context (a visual image) provides a cue about whether or not a prediction can be generated, rather than presenting participants with cues that indicate that a particular prediction is violated. Thus, while the existence of prediction in language processing has been convincingly demonstrated, to our knowledge no prior findings speak to the process of preactivating predicted representations.

In this study, we capitalized on evidence from a series of magnetoencephalography (MEG) experiments showing that visual cortex is sensitive to seemingly high-level factors (Dikker & Pykkänen, 2011; Dikker, Rabagliati, Farmer, & Pykkänen, 2010; Dikker, Rabagliati, & Pykkänen, 2009). These studies found that the visual M100 response, a very early sensory response generated in visual cortex, was sensitive to whether or not a prediction for a specific word or word category was satisfied. Dikker et al. (2009)

propose a Sensory Hypothesis to explain this finding: they suggest that early visual responses to word category violations and lexical-semantic mismatches follow from top-down modulation of visual cortex, resulting in the preactivation of form-features that are associated with the predicted syntactic category or word.

A crucial prediction of an account whereby these early sensory effects result from a mismatch with visual feature predictions is that changes in activation in visual cortex should occur before the onset of the critical word, resulting from the process by which predicted visual representations are preactivated.





In the present experiment, we asked this question by investigating brain activity as a function of context. Comparing highly predictive contexts (where one item has a high cloze-probability as compared to other items) to non-predictive contexts (where no single word has a high cloze-probability as compared to others), we expected to see more brain activity in visual cortex before the onset of (un)expected (i.e., matching or mismatching) words in high-cloze probability contexts, reflecting the preactivation of visual features. Previous studies have already shown that regions that are sensitive to prediction errors may also be recruited during the top-down predictive processing. Summerfield and Koechlin (2008), for example, compared predictive and non-predictive contexts in a low-level visual manipulation and found increased backward connectivity from Fusiform Gyrus to primary visual cortex in predictive contexts only, in addition to increased feedforward connectivity between these regions for prediction mismatches.

Investigating anticipatory processing requires an experimental design where visual/auditory input before the onset of the target word is maximally identical between conditions. Otherwise, effects in the pre-stimulus time-window for highly predictive vs. non-predictive contexts are confounded by lexical and other differences between the stimuli. Given that context is exactly the factor that is likely to trigger predictive processing in some cases (*he spread the warm bread with ___*) but not in others (*I like ___*), equating input across conditions is next to unfeasible. At the expense of somewhat departing from natural language processing, we used a very simple picture–noun matching task to approximate optimal conditions, as described in Dikker and Pykkänen (2011). Although different pictures were shown in each trial, crucially, input across conditions was held constant across conditions for a duration of 1500 ms between the presentation of the image and the onset of the target noun (see Materials), i.e., during the time-window of interest for predictive processing. Nouns either matched the image or they did not (see Table 1 in Section 2), and participants were engaged in a match/mismatch task. The function of the pictures was to constrain cloze-probability. For example, a picture of an apple was used to induce a strong prediction for the word *apple* in a subsequent noun phrase. A word like *banana* then violated this strong prediction. In addition to pictures denoting specific objects, there were images that could refer to any animal or any food item: A picture of a grocery bag stood for any word describing an edible or drinkable object, and a picture denoting Noah’s Ark functioned as a placeholder for any noun describing an animal. In other words, for trials showing pictures of specific objects, there was always a one-to-one mapping between the picture and the noun (predictive condition). In trials where participants saw either a grocery bag or Noah’s Ark, the picture could map onto a whole range of words, i.e., no specific word could be predicted (non-predictive condition).

Using these stimuli, a recent study (Dikker & Pykkänen, 2011) reported a visual M100 effect in MEG when comparing matching nouns to non-matching nouns, but only for predictive trials, i.e., when a specific word could be anticipated given a preceding image. They argued that in the predictive condition, but not in the non-predictive condition, participants generated expectations about the visual form of the words associated with the image. In line with predictive coding models (e.g., Friston, 2003) and visual attention

Table 1

Examples of experimental stimuli. Examples of experimental stimuli (80 per condition; 40 animals and 40 food/drink items).

+ / - PRED	PRIME	TARGET	+ / - MATCH
+ prediction for specific word (form)		the apple	+ MATCH
		the apple	- MATCH
- prediction for specific word (form)		the apple	+ MATCH
		the apple	- MATCH

models of biased competition (e.g., Desimone & Duncan, 1995), the mechanism underlying these expectations may be a process by which neuronal populations that encode predicted form-features are excited, while those encoding irrelevant features are simultaneously suppressed.

These mechanisms are described in Fig. 1 for cases where a strong prediction is violated. (For illustrative purposes only, 'form features' are here shown as letters.) During the presentation of the prime picture (left model brain), the lexical entry for "banana" is preactivated as a function of its predictability. This in turn triggers top-down modulation of visual cortex. This causes excitation of relevant form representations (blue bubbles; "a", "b", "n") and the suppression of competitors (e.g., "p", "l"). Then, during presentation of the unexpected target word "apple" (right model brain), visual analysis triggers the activation of the previously suppressed representations "p" and "l" (possibly in addition to a suppression of form representations "b" and "n"), resulting in enhanced activation of visual cortex in these cases as compared to cases where the prediction is satisfied.

The cartoon model in Fig. 1 not only describes how early sensory effects of expectancy violations may arise (Panel B), but it also describes the hypothesis that visual cortex should be more active for predictive trials than non-predictive trials *before* the onset of the word, indexing the preactivation of the visual word form associated with the predicted word (Panel A). Such a result would fit in with previous studies that have demonstrated top-down as well as predictive effects on visual processing (Albright & Stoner, 2002; Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Buetti, Bahrami, Walsh, & Rees, 2010; Lee & Mumford, 2003; Rao & Ballard, 1999; Stokes et al., 2009).

In addition to preactivation of visual cortex as a function of expectation, most models would predict that 'higher' cortical regions are involved in predictive processing. Although there exists no direct evidence pertaining to where contextual predictions in language processing might be generated, there are several brain areas that are plausible candidates.

Prefrontal cortex – Perhaps most prominently, various regions of prefrontal cortex have been suggested as likely sources of anticipatory processing (Bar, 2007; Bubic et al., 2010). Bar (2007) specifically proposes the involvement of medial prefrontal cortex

(mPFC) in generating predictions, an area that has been associated with cognitive control broadly, and evaluating potential outcomes in particular (Ridderinkhof & et al., 2004). Ventral regions of the medial prefrontal cortex have been implicated in anticipatory and top-down processing for visual object recognition (Bar & et al., 2006; Summerfield et al., 2006). Further, activity in anterior cingulate cortex (ACC) has been found to correlate with preparatory processing for upcoming perceptual events as well as the likelihood of prediction error (Brown & Braver, 2005). Prefrontal regions have moreover been implicated in the top-down modulation of visual cortex as a function of attention (Desimone & Duncan, 1995; Lamme, 2003; Gregoriou, Gotts, Zhou, & Desimone, 2009), and it has been suggested that enhanced phase synchronization of neuronal populations in prefrontal regions predict visual processing as well as behavioral responses (Engel, Fries, & Singer, 2001; Liang, Bressler, Ding, Truccolo, & Nakamura, 2002). In sum, we might expect recruitment of prefrontal areas as a function of predictive processing.

A few studies have explicitly investigated the connection between prefrontal areas and sensory regions in anticipatory processing. For example, Summerfield et al. (2006) investigated contextual prediction in resolving perceptual ambiguity in object identification and found an increase in top-down connectivity between prefrontal regions and occipito-temporal cortex depending on context. It is important to point out, however, that in this research "context" was defined very globally (in terms of experimental blocks) and was strictly induced by the experimental task, while in language processing, context is typically dynamic and local.

Temporal Cortex and Inferior Frontal Gyrus – As pointed out above, previous studies on object recognition have reported effects of predictive context in Fusiform Gyrus (Summerfield et al., 2006), arguably reflecting the preactivation of visual object representations. In the case of linguistic prediction, then, we might equally expect effects in regions that support linguistic representations. For lexical-semantic prediction, these areas are likely to include the mid-temporal cortex (MTC) and anterior as well as posterior inferior frontal gyrus (IFG) specifically, regions that have been associated with lexical access, retrieval, and selection respectively (see e.g., Lau, Phillips, and Poeppel (2008) for review).

In addition to investigating which brain regions are recruited in predictive processing, we explored whether sensitivity to prediction might be concentrated in specific frequency ranges. Previous evidence is consistent with the hypothesis that lexical-semantic predictive processing is specifically associated with activity in lower frequency ranges, in particular theta (4–7 Hz, Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005; Cavanagh, Frank, Klein, & Allen, 2010; Davidson & Indefrey, 2007; Hald, Bastiaansen, & Hagoort, 2006; Summerfield & Mangels, 2005). For example, while local computations are typically associated with higher frequency (gamma) activity, it has been suggested that processes of top-down modulation surface in the theta frequency range (Von Stein, Chlang, & Konig, 2000), and recent research by Cavanagh and colleagues has found that mPFC activity concentrated in the theta band was correlated with prediction error responses (Cavanagh et al., 2010). Studies have further associated theta activity with lexical-semantic processing (Davidson & Indefrey, 2007; Hald et al., 2006). For example, Bastiaansen et al. (2005) argue that theta activity in left-temporal cortex may index the activation of a network involved in lexical-semantic retrieval processes.

In sum, this study investigated brain responses associated with anticipating upcoming words by comparing highly predictive contexts to non-predictive contexts using a picture-word matching task in MEG. If anticipatory processing takes the form of preactivating predicted representations, we would expect more brain activity when a specific word can be anticipated, concentrated in those brain regions that have been previously found to support

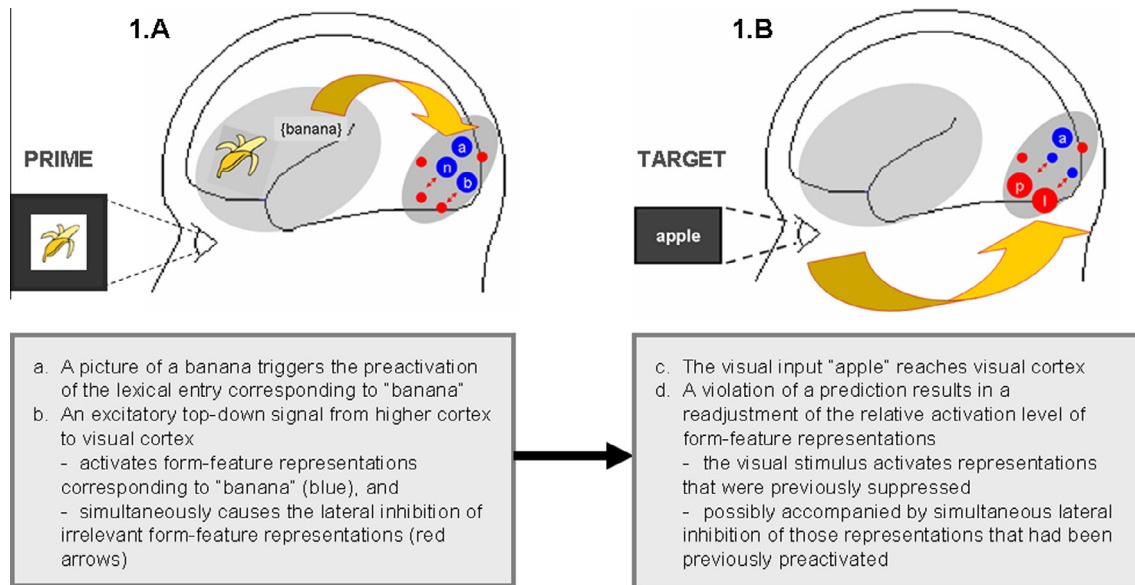


Fig. 1. The sensory hypothesis. A cartoon brain model representing the underlying top-down mechanisms that might explain expectation and violation effects during the M100 response. During the presentation of the prime picture (left model brain), the lexical entry for "banana" is preactivated, which triggers top-down modulation to visual cortex. This causes the excitation of relevant form-representations (blue bubbles; *a, b, n*) and the suppression of competitors (e.g., *p, l*). Then, during presentation of the unexpected target word "apple" (right model brain), visual analysis triggers the activation of the previously suppressed *p* and *l* (possibly in addition to a suppression of *b* and *n*), resulting in enhanced activation of visual cortex in these cases as compared to cases where the prediction is satisfied.

relevant representations (such as left-temporal cortex for lexical- semantics and visual cortex for form features). Further, if the hypothesized role of the medial prefrontal cortex in prediction generation (Bar, 2007) extends to language, then we might expect enhanced mPFC activation triggered by our predictive contexts.

2. Materials and methods

2.1. Participants

22 right-handed participants with normal or corrected-to-normal vision participated in this study (8 female; mean age: 27).

2.2. Materials

80 different pictures and nouns were presented in four conditions (exemplified in Table 1).

Nouns (half of which matched the preceding picture) were presented either after a picture denoting a specific object (+Predictive) or after a picture that stood for a semantic field (–Predictive; Noah's Ark for "animals" and a grocery bag for "food"). Images were shown twice in the +Predictive condition and 40 times in the –Predictive condition. Visual properties of words that violated specific predictions were maximally distinct from those of the predicted word (see Dikker and Pykkänen (2011) for details). The experiment consisted of two blocks: For reasons explained in Dikker and Pykkänen (2011), Block 1 contained only +Predictive trials. In Block 2, +Predictive and –Predictive trials were intermixed. Since in the current study we are interested in the contrast between +Predictive and –Predictive trials, here we only report data from Block 2 (see Dikker and Pykkänen (2011) for results pertaining to the full design). The +Predictive trials in Block 2 were an exact repetition of Block 1. As a result, participants were already familiarized with all the +Predictive picture–noun pairs by the beginning of Block 2, thus boosting the predictive nature of the images in the +Predictive condition.

As exemplified in Fig. 2, presentation was held constant across the +PRED (+Predictive) and –PRED (–Predictive) conditions for a duration of 1500 ms between the offset of the picture (presented for 900 ms) and the onset of the target noun, i.e., the time window of interest for comparing activity between –Predictive and +Predictive conditions preceding the onset of the noun. Although the pictures constituted different visual inputs between conditions, brain activity associated with picture processing subsided well before the onset of the noun phrase, consistent with previous findings on picture processing (West & Holcomb, 2002; Willems, Ozyürek, & Hagoort, 2008).

2.3. Procedure

Participants lay in a dimly lit, magnetically shielded room for the duration of the experiment. Using PsyScope X, stimuli were projected onto a screen at ~50 cm from the participant's head. Both pictures and words were shown against a 75% gray background, with words presented in white in non-proportional Courier font (size 28). During the experiment, participants performed a match/mismatch task (see stimuli in Table 1). For each trial, an image was first shown for 900 ms. After this, a 300 ms blank screen appeared, followed by a fixation cross (300 ms) and then the noun phrase (word-by-word, 300 ms on/off). Participants indicated whether the noun phrase accurately described the preceding picture when a question mark appeared at the end of a trial (MATCH: left index finger; MISMATCH: left middle finger). A feedback screen showed the correct answer. Initiation of the next trial was self-paced.

Before entering the magnetically shielded room, participants were shown all picture primes and corresponding nouns, and were familiarized with the task (30 practice trials total). The experiment itself consisted of two blocks. During Block 1 of the experiment, participants only saw +Predictive trials (160 trials total). Block 2 consisted of both +Predictive and –Predictive trials (320 trials total; +Predictive trials repeated the ones in Block 1, but randomly

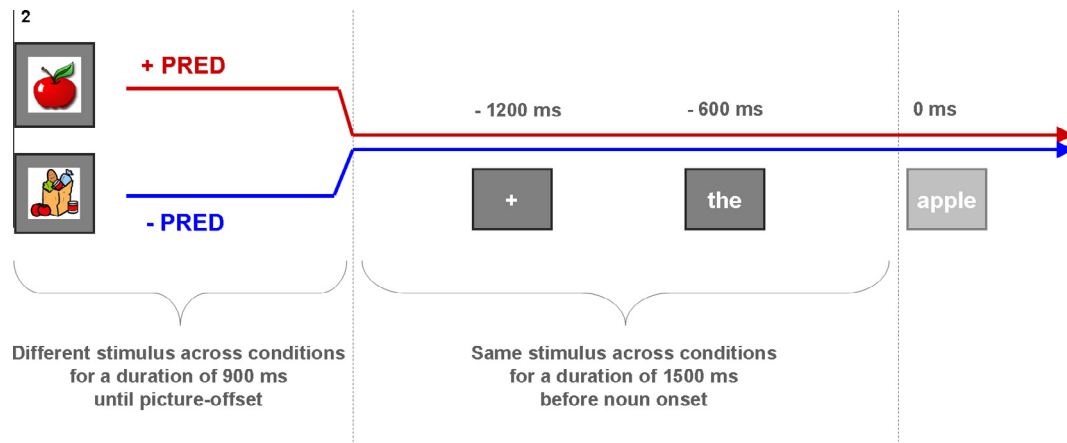


Fig. 2. Timing of stimulus presentation. The red line marks predictive contexts (presentation of a specific object); the blue line indicates non-predictive contexts (presentation of a grocery bag or Noah's Ark). Pictures were presented for a duration of 900 ms (distinct between contexts), followed by 1500 ms of identical input across contexts.

presented). The entire experiment, including preparation, training, and recording, lasted approximately 45 min.

2.4. Data acquisition

Neuromagnetic fields were recorded continuously with a whole-head, 157-channel axial gradiometer array (Kanazawa Institute of Technology, Kanazawa, Japan) (sampling rate: 1000 Hz; 0–200 Hz band; 60 Hz notch filter).

2.5. Data analysis

2.5.1. Pre-processing

Three participants showed low signal-to-noise ratio in the MEG data and were excluded from the analysis. Since this study focuses on visual processing, we additionally excluded four participants who failed to show canonical early visual brain responses, as determined based on visual inspection of the M100 and M170 field patterns (see e.g., Pykkänen & Marantz, 2003) in the grandaveraged sensor data for each participant. Prior to averaging, MEG data were cleaned of artifacts in BESA 5.1 by excluding trials for which the maximum amplitude exceeded a threshold of 4000 fT. In addition, trials with incorrect judgments were excluded, resulting in the total exclusion of 15% of the data on average per subject. Data were averaged by condition over a 3000 ms epoch, time-locked to the onset of the target noun (2400 ms pre-stimulus; 600 ms post-stimulus) after baseline-correcting each trial by applying a low-cutoff forward filter (.01 Hz).

2.5.2. Whole-brain minimum norm estimates

After averaging, data was bandpass-filtered at 1–40 Hz as well as four canonical frequency ranges: Beta (13–30 Hz), Alpha (8–12 Hz), Theta (4–7 Hz), and Delta (.1–3 Hz).

To investigate event-related pre-stimulus brain activity associated with predictive processing, we compared whole-brain minimum norm estimates (MNEs) of neural activity for predictive vs. non-predictive contexts for each of these bands separately. Source estimates were calculated in BESA 5.1. MNEs were based on activity from 1426 regional sources, evenly distributed in two shells 10% and 30% below a smoothed standard brain surface. Regional sources can be seen as two orthogonally oriented dipoles in the same location and total activity was defined in terms of the root mean square (RMS) of the source activities of its two components, after which pairs of dipoles at each location were averaged and the larger value from each source pair was selected, resulting in 713

non-directional sources. Minimum norm images were depth-weighted as well as spatio-temporally weighted, using a signal subspace correlation measure (Mosher & Leahy, 1998).

Phase-locked activity in each frequency range for +Predictive vs. –Predictive conditions was compared sample by sample for every source time point using a paired *t* test. To reduce the chance of Type I errors, differences between conditions in the prestimulus time-window were considered reliable only if they persisted for at least 40 consecutive time-points and in 10 adjacent sources.

3. Results

3.1. Behavioral results

2 (Context: –Predictive vs. +Predictive) by 2 (Congruence: Match vs. Mismatch) within-subjects ANOVAs showed a main effect of Context both for accuracy ($F(1,14) = 11.742, p = .004$) and for reaction times ($F(1,14) = 56.743, p < .001$): participants were faster and committed less errors overall for the +Predictive conditions than the –Predictive conditions. (For further details regarding the behavioral results, see Dikker & Pykkänen, 2011).

3.2. MEG data

3.2.1. Picture time-window

Our primary time-window of interest was the period right before the onset of the target noun. However, to make sure that any effects in that time-window did not constitute spill-over from activity related to picture processing, we also looked at the trials' first 1800 ms. During the presentation of the picture, we observed a widely distributed increase in brain activity for predictive compared to non-predictive pictures, possibly due to the participants' familiarity with the images (each image was repeated 40 times in the non-predictive condition, but only twice in the predictive condition). These differences in brain activity between +Predictive and –Predictive conditions during the presentation of the picture lasted around 600 ms (in line with previous findings on image processing; West & Holcomb, 2002; Willems et al., 2008), and subsided well before the onset of the noun phrase (see also Fig. 5, Panel 3). Importantly, there were no reliable differences in brain activity between conditions from –1800 ms to –450 ms before the onset of the target word. The results presented below focus on the interval directly preceding the noun, i.e., during the presentation of the determiner “the.”

3.2.2. Pre-noun and post-noun interval

MEG results for the pre-stimulus interval beginning at –600 ms are presented in Figs. 3 and 4. In each figure, Panel 1 shows whole-

brain minimum norm estimates (MNEs) for prestimulus activity comparing predictive and non-predictive contexts. Panel 2 displays post-stimulus whole-brain minimum norm estimates of changes in

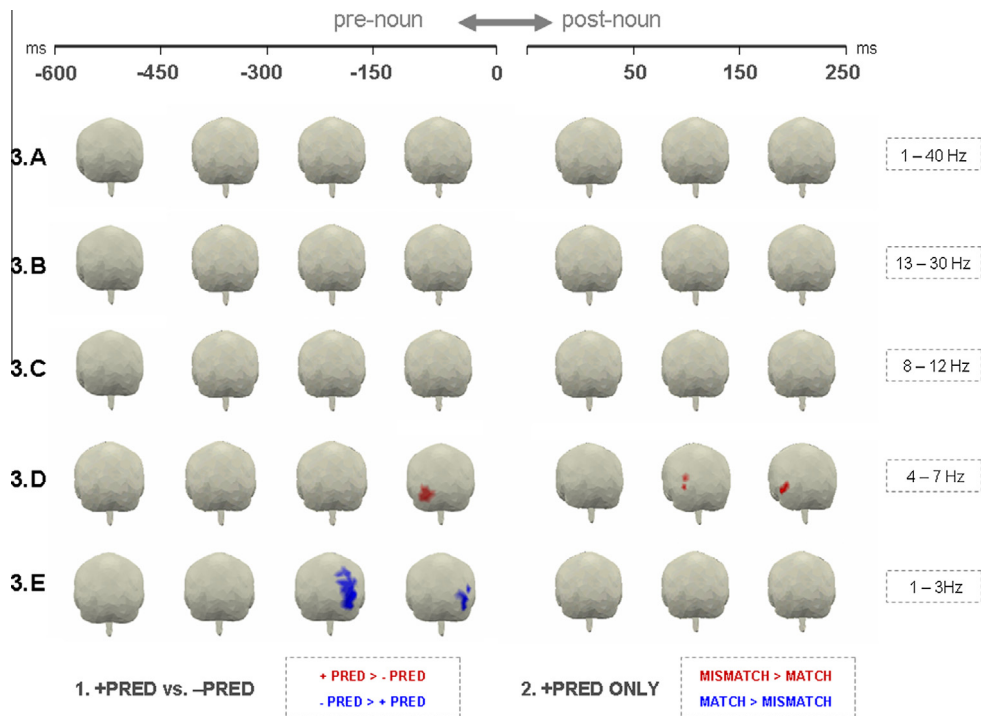


Fig. 3. Prestimulus and target word visual activity: different frequency bands. Results of the whole-brain analysis over MNEs for data filtered at 1–40 Hz (3A), 13–30 Hz (Beta; 3B), 8–12 Hz (Alpha; 3C), 4–7 Hz (Theta; 3D), and 1–3 Hz (Delta; 3E) respectively. Colored regions indicate areas where amplitude differences (in nAm) were reliable. Panel 1. Predictive vs. non-predictive contexts displayed from –600 to 0 ms before the onset of the target noun. Red: more activity for +Predictive contexts than –Predictive contexts; blue: less activity for +Predictive contexts. Threshold: $p < .05$ for ≥ 40 ms and ≥ 10 spatial neighbors. Panel 2. Matching vs. Mismatching nouns in Predictive contexts displayed from –50 to 550 ms after the onset of the target noun. Red: more activity for the Mismatch condition than Match condition; Blue: less activity for the Mismatch conditions. Threshold: $p < .05$ for ≥ 40 ms and ≥ 10 spatial neighbors.

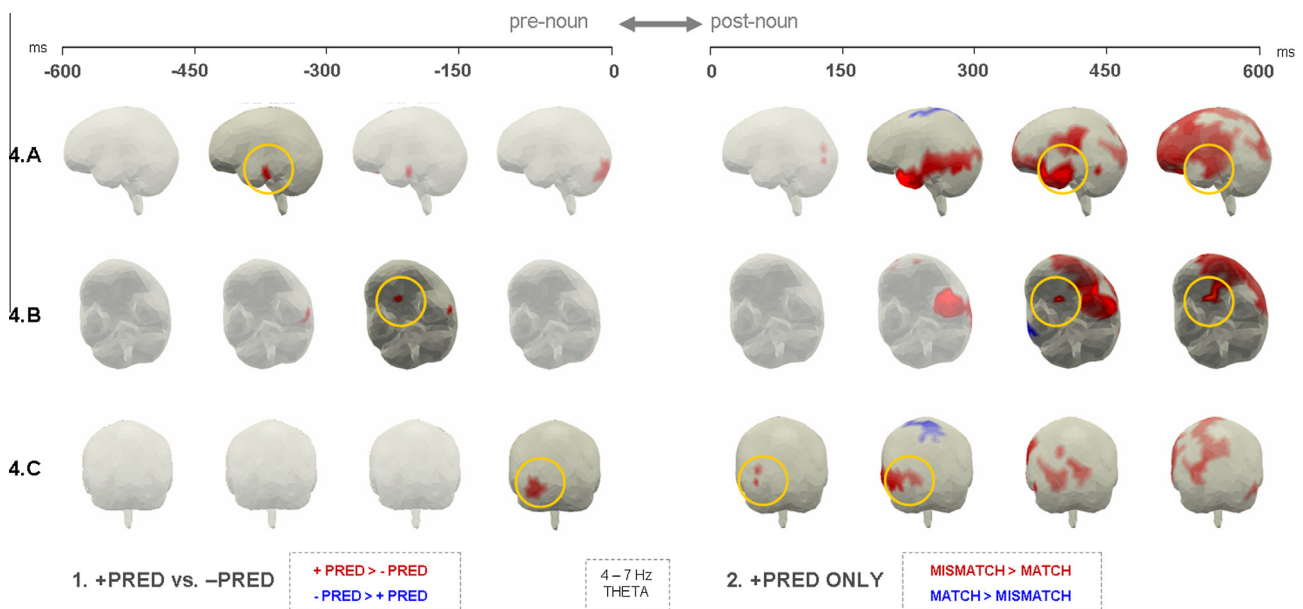


Fig. 4. Pre-noun and post-noun whole-brain comparison in theta. Whole-brain minimum norm estimates for data bandpass filtered between 4 and 7 Hz (theta range). Colored regions indicate areas where amplitude differences (in nAm) were reliable. Panel 1. Predictive vs. non-predictive contexts displayed from –600 to 0 ms before the onset of the target noun, showing (A) a left-temporal view, (B) a ventral view, (C) a posterior view of the model brain. Red: more activity for +Predictive contexts than –Predictive contexts; blue: less activity for +Predictive contexts. Threshold: $p < .05$ for ≥ 40 ms and ≥ 10 spatial neighbors. Panel 2. Matching vs. Mismatching nouns in Predictive contexts displayed from –50 to 550 ms after the onset of the target noun. Red: more activity for the Mismatch condition than Match condition; Blue: less activity for the Mismatch conditions. Threshold: $p < .05$ for ≥ 40 ms and ≥ 10 spatial neighbors.

brain activity for the match vs. mismatch comparison in the +Prediction conditions only. We here only show results for Block 2 and refer to Dikker and Pykkänen (2011) for results pertaining to the full design. (Dikker & Pykkänen, 2011 found no differences in the magnitude of early visual responses to (mis)matching nouns between Block 1 and Block 2, i.e., participants did not appear to develop sensitivity to visual properties of (mis)matching nouns as a task-strategy.) Colored regions mark brain areas where differences in brain activity for each comparison were reliable (see Section 2.5.2).

Whole-brain analysis: all frequency bands – Results of the whole-brain minimum norm estimates are shown in Fig. 3 for the five frequency ranges that were investigated. Colored regions indicate those sources where differences between conditions were reliable (threshold: $p < .05$; 40 ms; >10 adjacent sources) No effects of context were observed for data filtered at 1–40 Hz, nor at the alpha or beta ranges (Fig. 3A–C respectively). Differences in brain activity before stimulus onset as a function of context only surfaced for data filtered at the lower frequency ranges (Fig. 3D and E). In the theta range, we saw enhanced activity for predictive contexts as compared to non-predictive contexts in visual cortex right before the onset of the noun. In the delta range, in contrast, long-lasting enhanced activation of visual regions was observed in non-predictive contexts.

As can be seen in Panel 2, effects of congruency in visual areas during the presentation of the noun were seen in theta, but not delta (please see Dikker and Pykkänen (2011) for a detailed description of effects of congruency in both +Predictive and –Predictive conditions). To investigate whether delta and theta were indeed differentially sensitive to congruency, we ran

frequency (theta vs. delta) \times congruency (+Predictive/Match vs. +Predictive/Mismatch) ANOVAs over millisecond-by-millisecond activity extracted from the visual region that exhibited sensitivity to context in the pre-stimulus window in each frequency band (see Fig. 3, pre-noun window). No congruency \times frequency interactions were observed for any of the time-points between 0 and 200 ms post-noun onset.

In sum, the data shown in Fig. 3A–E suggest that brain activity concentrated in the theta-range in particular is sensitive to prediction, showing visual effects both before the onset of the noun as a function of context, and during the presentation of the noun as a function of whether or not a strong prediction was satisfied.

Whole-brain analysis: Theta range – Fig. 4 shows whole-brain MNEs for data filtered between 4–7 Hz (theta range), with a left-hemisphere view (4A), a ventral view (4B), and a posterior view (4C) respectively. First and foremost, we see that context affects occipital activation exactly as the Sensory Hypothesis would predict: right before the onset of the noun, more activity is seen in visual cortex for predictive as compared to non-predictive contexts (Fig. 4C).

In addition to visual cortex, two other regions were more active in predictive than non-predictive contexts in the prestimulus time-window. First, around 350 ms before the onset of the noun, an effect emerges in the left mid-temporal cortex (MTC; Fig. 4A), a region that is assumed to participate in lexical access. Around the same time-point, we also observe an effect in the ventro-medial prefrontal cortex (vmPFC; Fig. 4B; see also Fig. 5.2A, which shows that the first effect in vmPFC emerges around 400 ms), a region that has been implicated in top-down modulation, attention and prediction error responses (as discussed in Section 1).

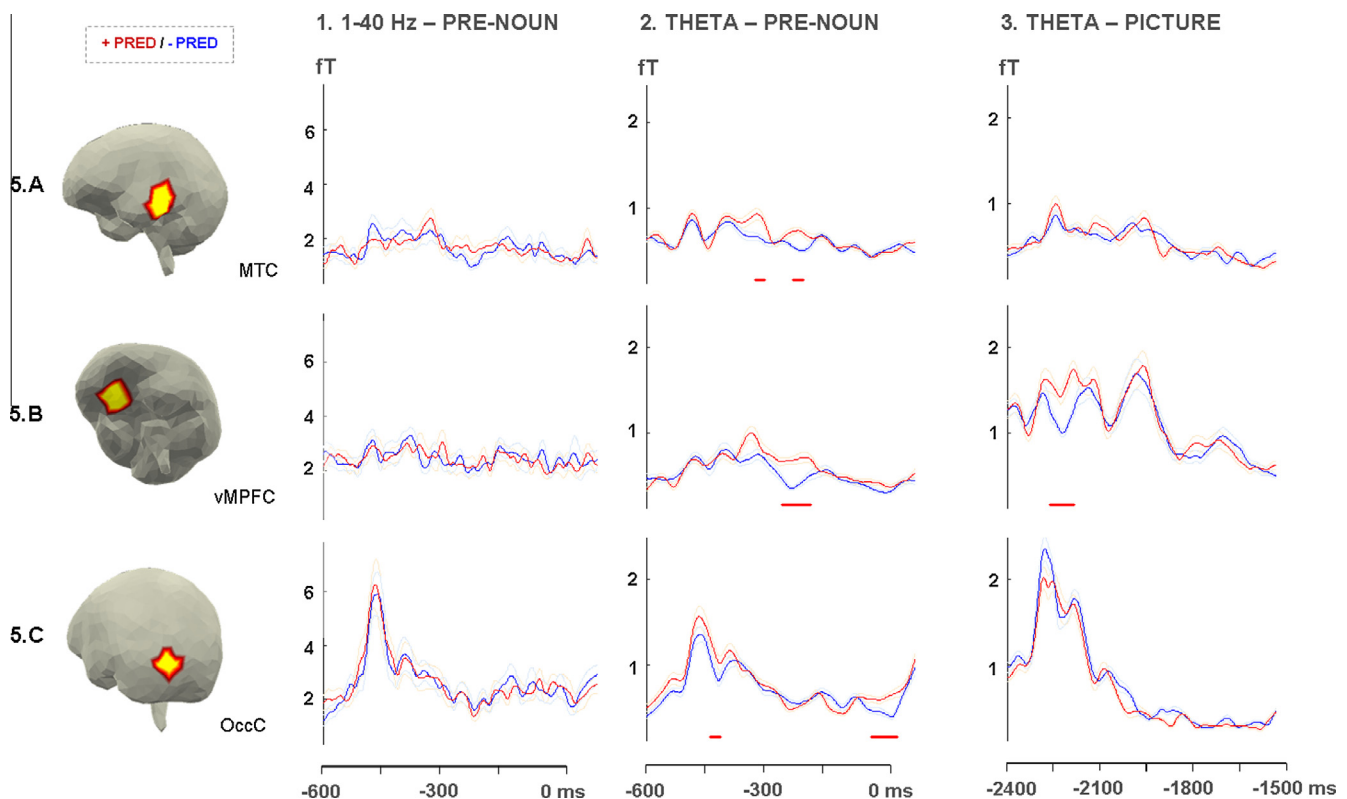


Fig. 5. By-region timecourses: theta and 1–40 Hz activity. Average by-region activity for 1–40 Hz (Panel 1) and theta (Panel 2). Activity was extracted from regions that showed reliable differences in the whole-brain MNEs in theta (Fig. 4): mid-temporal cortex (MTC; 5A), ventro-medial prefrontal cortex (vmPFC; 5B), and occipital cortex (OccC; 5C). +Predictive: red; –Predictive: blue (error-bars are indicated with light colored waveforms). Red lines indicate time-points where activity was reliable for at least 40 ms consecutively ($p < .05$). Panel 1 (1–40 Hz) and Panel 2 (theta): Predictive vs. non-predictive contexts from –600 to 0 ms before the onset of the target noun. Panel 3 (theta): Theta: Predictive vs. non-predictive contexts from –2400 to –1500 ms before the onset of the target noun, during picture presentation. Note the y-scale difference between 5A and 5B/C respectively.

Crucially, these brain areas also responded to whether or not a given noun matched the prediction (Panel 2), although mismatch responses were more broadly distributed than in the prestimulus window.

Timecourse activity by region – To illustrate theta vs. 1–40 Hz phase-locked activity for +Predictive and –Predictive trials, Fig. 5 displays the average timecourses of activity extracted from the three regions that showed reliable differences by Context in the whole-brain theta analysis (see Fig. 4): mid-temporal cortex (MTC; Fig. 5A), ventro-medial prefrontal cortex (vmPFC; Fig. 5B), and Occipital Cortex (OccC; Fig. 5C). Panel 1 shows activity in the pre-noun window in these regions, and Panel 2 shows the same comparison for 1–40 Hz. +Predictive trials are displayed in red, –Predictive trials in blue (error-bars are indicated with semi-transparent shading). Red bars mark those time-points where activity was reliable for at least 40 ms consecutively ($p < .05$).

As can be seen when comparing Panel 1 and Panel 2, differences in these regions by Context were only observed in theta, and not in the 1–40 Hz range.

Panel 3, displaying +Predictive vs. –Predictive activity during the presentation of the picture for each region, shows that mid-temporal cortex and occipital cortex, which were sensitive to context in the 400 ms time-window before noun-onset (Panel 1) did not respond differently to the +Predictive vs. –Predictive image types during picture presentation (Panel 3). This tentatively suggests that the differences between +Predictive and –Predictive trials right before noun onset were not due to reactivating the preceding images.

In sum, the present results revealed (a) more activity before the presentation of the target noun in predictive contexts as compared to non-predictive contexts in the left mid-temporal cortex (implicated in lexical access), ventro-medial prefrontal cortex (associated with e.g., top-down processing, multi-sensory integration and prediction error responses), and visual cortex (hypothesized to index the preactivation of predicted form features), successively; (b) effects of predictive processing appeared to be concentrated in the theta frequency band; and (c) the same brain regions that exhibited enhanced activation for predictive contexts before the onset of the noun showed effects of congruence during the target word. Finally, the fact that participants were faster for +Predictive stimuli supports the hypothesis that being able to factor in the (possible) identity of an upcoming stimulus has a behavioral advantage.

4. Discussion

The goal of this study was to identify the neural correlates of predictive language processing *before* predicted words are presented. We found that visual cortex, left temporal cortex, and ventro-medial prefrontal cortex showed enhanced activation in predictive contexts when compared to contexts where no prediction for one specific word could be generated. These effects were concentrated in the theta band. Moreover, we saw that the same brain regions that exhibited such enhanced activation before the onset of the noun showed effects of congruence during the presentation of the target noun. This is exactly the pattern of activation that would be expected under a prediction account: arguably, predictive processes feed back from higher to lower cortical regions, whereas prediction error—or mismatch—responses follow a bottom-up processing stream from low-level to higher-level representations (Friston, 2003; Summerfield & Koechlin, 2008).

Temporal and visual cortex – In all results presented above, we saw effects of prediction in the left mid-temporal cortex, followed by a prediction effect in visual cortex. This set of findings provides relatively direct evidence in support of the Sensory Hypothesis: More activity in visual cortex was seen for highly predictive

contexts compared to non-predictive contexts, right before stimulus-onset, possibly indexing the preactivation of form features associated with the predicted word. As for the left mid-temporal cortex, we pointed out above that it has been proposed to support lexical access (see e.g., Lau et al. (2008) and Pykkänen and Marantz (2003) for review). Thus, the enhanced activation of the left mid-temporal cortex before stimulus-onset is likely to reflect preactivation of the predicted lexical representation, based on which form feature estimates are generated. In other words, our findings suggest preactivation as a result of lexical–semantic prediction at both the level of word form features (visual cortex) and lexical representation (following research arguing that left mid-temporal cortex is involved in lexical access). All effects were left-lateralized, which would be expected under a preactivation account: lexical–semantic processing is typically left-dominant and the early visual effects of predictability in our previous studies were similarly slightly left-lateralized (Dikker & Pykkänen, 2011; Dikker et al., 2009, 2010).

Prefrontal cortex – Above, we mentioned a number of medial prefrontal regions as plausible candidates for predictive processing. Our results show activity associated with anticipatory processing in the ventral part of the mPFC in particular, an area that has been associated with a range of cognitive functions, including attention (Desimone & Duncan, 1995), predictive processing (Bar, 2007), and top-down effects in object perception (Bar & et al., 2006). Many scholars have suggested that prefrontal cortex serves as an integrative vehicle between different cortical regions (Miller & Cohen, 2001), and as such may have a crucial linking function between distinct levels of representation (see e.g., Wood and Grafman (2003) for a review). This is also consistent with research suggesting that the vmPFC may play a vital role in linguistic composition (Bemis & Pykkänen, 2011; Brennan & Pykkänen, 2008, 2010; Pykkänen & McElree, 2007). Moreover, a recent study investigating speaker–listener neural coupling found that better story retention/understanding was correlated with activation patterns in mPFC, which the authors argue may index successful prediction (Stephens, Silbert, & Hasson, 2010). Based on this set of evidence, we suggest that in the present study vmPFC may have facilitated the communication of lexical–semantic expectations from temporal to occipital regions, i.e., the translation of lexical–semantic representations into form-based estimates.

Mechanisms of prediction – We follow previous proposals (e.g., Bar, 2007) in assuming that the ‘proactive brain’ draws on different sources of information in its attempt to preactivate upcoming input where possible: In the case of word-by-word reading studies on prediction (such as the ones discussed in the Introduction; e.g., DeLong et al., 2005; Van Berkum et al., 2005) this information is extracted from the preceding linguistic context. In our study and those using a visual world paradigm (e.g., Altmann & Kamide, 1999) this information can be drawn from the visual context.

The functional explanation proposed here for the effects found in the vmPFC fits readily within so-called ‘sharpening models’ of preactivation (or priming; Grill-Spector et al., 2006). For example, the *biased competition model of visual attention* (e.g., Desimone, 1996; Desimone & Duncan, 1995), which is arguably computationally equivalent to *predictive coding* (Friston, 2003; see Spratling, 2008), describes how top-down excitatory signals from pre-frontal to visual cortex may bias the processing of certain representations over others. Under this model, the excitatory signal acts to enhance the activation level of neuronal populations that encode relevant representations and simultaneously suppress, by way of lateral inhibition, activity in neurons that represent irrelevant representations. For predictive contexts then, increased activation of visual cortex before the onset of the noun would reflect top-down induced changes in the relative activation level of neuronal population therein. In non-predictive contexts, in contrast, no top-down modulation of visual cortex takes place.

A model of this type also provides an explanation for why Dikker and Pyllkkänen (2011) found no M100 effects in the non-predictive condition: in the absence of any priors that trigger the selective preactivation of certain visual features, early visual processing of any incoming word will induce equal processing cost. Increased visual processing cost occurs only when such priors are violated, as was exemplified in Fig. 1 in the Introduction.

It is worth noting that we wish to remain agnostic with respect to the distinction between priming and prediction at the mechanistic level in the context of this study. The compatibility of our results with sharpening models of priming in fact suggest that predictive preactivation and preactivation as a result of priming may well be neurologically equivalent (this is tentatively supported by results from e.g., Federmeier & Kutas, 1999). We leave it to future studies to investigate possible differences between priming and prediction in more detail.

Timing of preactivation – In theory, participants could be activating the word and its corresponding visual features as soon as the picture becomes available, and then keep these representations active throughout the trial. However, in the present study sensory effects did not arise until right before the onset of the noun. This could in part be due to the fact that there was intervening linguistic material between the picture and the noun, or it may be more costly to maintain sensory representations active across a long temporal interval than to only activate them right before they become relevant (when processing the noun). Potentially, the preactivation of form features associated with nouns is triggered by the presentation of a determiner (as this is a natural sequence of linguistic elements), but future studies will have to disentangle possible explanations for the timing of these effects.

Prediction and language production – Some scholars have argued that predictive language processing recruits the language production network (Pickering & Garrod, 2007). Under this hypothesis, participants in our experiment could be engaging in silent naming of the images, as such triggering the preactivation of corresponding linguistic representations. While we do not discard this as a possibility, we believe that silent production alone cannot explain our findings, as it is unclear how this account would predict increased activity in visual cortex right before the onset of the noun.

Preactivation vs. reactivation – It is possible that participants reactivated a mental image of each picture right before the onset of the noun. Prior research has suggested that brain responses to mental imagery are very similar, if not identical, to responses to the physical presentation of the imagined stimulus (e.g., Tian & Poeppel, 2010). Thus, one would expect qualitatively similar context-based differences during the picture as well as right before noun-onset. However, as shown in Fig. 5 Panel 1 vs. Panel 3, the visual cortex region and mid-temporal areas that responded differently to predictive vs. non-predictive trials right before noun-onset were not sensitive to these differences during the presentation of the picture. This tentatively supports the conclusion that the pre-noun effects reflect word form preactivation, rather than just mental image reactivation alone.

Lower frequency ranges and prediction – Future studies will have to investigate the oscillatory properties of predictive processing, but our results suggest that predictive processing may only be observable when focusing on lower frequency ranges. As pointed out in the Introduction, the concentration of preactivation effects in the theta frequency band fits in nicely with previous findings suggesting that both lexical–semantic activation and top-down processes are specifically associated with activity in this frequency range (Bastiaansen et al., 2005; Cavanagh et al., 2010; Davidson & Indefrey, 2007; Hald et al., 2006; Summerfield & Mangels, 2005). In addition, there exists research suggesting that activity in the theta band plays an important role in the functional coupling between frontal and posterior regions (Summerfield & Mangels,

2005) and Cavanagh and colleagues found prediction error effects in theta (Cavanagh et al., 2010). Previous research has additionally reported sensitivity to prediction error in higher frequency ranges (e.g., Arnal et al., 2011). Under the present analysis approach, we cannot rule the possible contribution of higher frequency activity to effects of congruency: by-condition differences in e.g., the gamma range are often washed out when looking at event-related, phase-locked activity (e.g., Pantev, 1995). However, since the focus of our study was to look at preactivation effects rather than congruency effects, we leave it to future studies to explore the relationship between prediction error responses in gamma and theta respectively.

We further saw that there was relatively more activity for non-predictive contexts before stimulus-onset in the delta frequency band. Such enhanced activity for non-predictive contexts could index an increased level of uncertainty about the upcoming stimulus, possibly triggering enhanced attention to the stimulus (Kirmizi-Aslan, Bayraktaroglu, Gurvit, Keskin, Emre, & Demiralp, 2006). Crucially, however, there were no reliable congruency effects in delta (although difference between theta and delta should be interpreted with caution, since there was no reliable frequency-by-congruency interaction). As discussed in the Introduction, we argue that predictive processing distinguishes itself from global attention mechanisms in that only the former targets a specific percept or mental representation. Global attentional shifts may nevertheless play a facilitating role in predictive processing, perhaps by optimizing conditions for preactivation mechanisms (see e.g., Summerfield & Egner, 2009 for a discussion on the relationship between attention and prediction). This explanation, however, remains tentative at this point and the exact relationship between attention and prediction, as well as the contribution of activity at different frequency ranges to each, requires further investigation.

A final note is in place to re-emphasize that picture–word matching tasks with long-lag intervals are not fully representative of natural language processing. While resolving linguistic references does often involve matching words to objects in the visual world around us (consider “can you hand me the . . .” at the dinner table), future studies will have to test whether our findings extend to more ecologically valid circumstances.

5. Conclusion

In the current study, brain activity was modulated by whether or not a specific noun could be predicted given a picture prime: *before* the noun was presented, predictive contexts triggered more activity first in ventro-medial prefrontal cortex and left-temporal cortex, and then in visual cortex. This finding suggests that predictive language processing recruits a top-down network where predicted words are activated at different levels of representation, from more ‘abstract’ lexical–semantic representations in temporal cortex, all the way down to visual word form features. During the presentation of a noun, the same network of brain areas was recruited when a prediction was violated. To our knowledge, this study is one of the first to directly investigate the anticipatory stage of predictive language processing, supporting evidence in favor of the widely held assumption that language processing is highly predictive and top-down in nature.

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