



Long-range neural synchronization supports fast and efficient reading: EEG correlates of processing expected words in sentences

Nicola Molinaro ^{a,*}, Paulo Barraza ^b, Manuel Carreiras ^{a,c}

^a BCBL, Basque center on Cognition, Brain and Language, Donostia/San Sebastian, Spain

^b CIAE, Centro de Investigación Avanzada en Educación, Universidad de Chile, Santiago, Chile

^c Ikerbasque, Basque Foundation for Science, Bilbao, Spain

ARTICLE INFO

Article history:

Accepted 20 January 2013

Available online 26 January 2013

Keywords:

ERPs

Phase-locking value

EEG gamma synchronization

EEG theta synchronization

Anticipatory processes

Reading

ABSTRACT

Word reading is heavily influenced by the information provided by previous context. In this study, we analyzed the neurophysiological bases of sentence reading through the EEG activity elicited during reading the same word embedded in differently constraining contexts: a) a low-constraining context; b) a high-constraining semantic compositional context; c) a high-constraining collocational context in which the item was in final position of a multi-word fixed-order expression. Cloze-probability of the two high-constraining contexts was equated. *Before* reading the target word we observed increased EEG gamma phase synchronization for the high-constraining compositional context and increased EEG theta synchronization for the collocational context (both compared to the low-constraining condition). *After* reading the target word we observed increased frontal positive EEG evoked activity (~220 ms) for the high-constraining compositional context but an even earlier (~120 ms) effect for the high-constraining collocational condition that was distributed over the scalp. A positive correlation was found only between the increased theta synchronization and the early EEG effect for the high-constraining collocational condition. Results indicate that long-range frontal–occipital interactions in the theta band – indexing working memory operations – support early visual–orthographic analysis of an incoming stimulus (such as the expected word); gamma-phase synchronization better represents binding operations between feed-forward activation and matching feedback. These data suggest that internal linguistic knowledge stored in long-term memory – if unambiguously pre-activated – supports the low-level perceptual processes involved in reading.

© 2013 Elsevier Inc. All rights reserved.

Introduction

Expectation-related effects in language comprehension have been widely reported in the neurocognitive literature for both reading (Kutas and Hillyard, 1984) and listening (Connolly and Phillips, 1994). “Anticipatory” processes have strong benefits for language comprehension in that they allow fast on-line integration of a considerable amount of information. This implies that during comprehension, the identification/recognition of a word and its related meaning could be strongly affected by the context in which it appears.

Empirically, it has been demonstrated that such contextual influence critically affects the form-to-meaning mapping of a word at multiple levels of processing. Early EEG (electroencephalogram) reading experiments focusing on the semantic fit of a word with its previous context showed modulations of event-related EEG activity (ERP, Event Related Potentials) in the 200–600 ms time range (Kutas and Hillyard, 1984): words in semantically high constraining contexts (compared to words

in low constraining contexts) show reduced negative amplitudes starting ~250 ms post-stimulus onset. Since this event-related activity correlates with lexical–semantic factors, it has been suggested to reflect the facilitated lexical–semantic processing of that word (Kutas and Federmeier, 2000; Lau et al., 2008).

However, more recent findings have led to debate concerning the possibility that highly constraining sentence contexts could determine brain reactions earlier in time. A variety of studies have shown early influence of both lexical/semantic (Dambacher et al., 2009; Federmeier and Kutas, 2001; Kim and Lai, 2012; Penolazzi et al., 2007; Sereno et al., 2003) and syntactic (Dikker et al., 2009, 2010) factors already within 100 to 200 ms post-stimulus word onset. Such effects would be related to the influence of the linguistic context on the initial processing of low-level visual features. One account of these early effects is that activation would percolate top-down influencing the visual–orthographic analysis of the stimulus (*top-down sublexical modulation hypothesis*): mechanisms that compare top-down predictions about low-level form features against the actual input would be responsible for differential sublexical processing (Dikker et al., 2010; Federmeier and Kutas, 2001; Kim and Lai, 2012). These effects could be explained by theoretical models of visual word recognition that postulate the presence of

* Corresponding author at: BCBL, Basque center on Cognition, Brain and Language, Paseo Mikeletegi 69, 2nd Floor, 20009, Donostia, Spain.

E-mail address: n.molinaro@bcbl.eu (N. Molinaro).

recurrent interactions across levels of processing: some cognitive frameworks have stressed the importance of cascading feedforward–feedback activation required for fine-grain analysis of a printed word (Grainger and Holcomb, 2009; McClelland and Rumelhart, 1981). In these visual word processing proposals, word-level semantic representations begin to be activated when substantial processing resources are still at the sublexical level of processing: early semantic activation could thus influence ongoing sublexical processing via feedback connections, especially when specific semantic activation has been previously enhanced by contextual information. The present study shows that interactions between high-level linguistic knowledge that is activated while reading a previous sentence context and sublexical low-level representations emerge from the earliest stages of visual word recognition during sentence reading.

In this framework, neurophysiological evidence of feedforward/feedback connectivity in the ventral visual brain pathway where attentive and pre-attentive vision interact provides a plausible brain architecture for such effects (Lamme and Roelfsema, 2000). In addition, direct anatomical connections between the extrastriate visual cortex and the lateral frontal association areas such as the inferior frontal gyrus have been found. Diffusion tensor imaging and histological studies of the human brain (e.g. Bernal and Altman, 2010; Wakana et al., 2004) have confirmed the presence of fibers within the superior longitudinal fasciculus that connect the primary visual cortices and the inferior frontal gyrus (Cornelissen et al., 2009; Pammer et al., 2004). This cortical substrate would support the presence of recurrent neuronal connections from ‘language regions’ to the more occipital regions of the cortex devoted to the visual analysis of a printed word. In fact, multiple possible pathways seem to be involved in the recognition of a visual stimulus (Bar et al., 2006): an initial increase of activation in the occipital regions would lead to increase of activation (~130 ms) in frontal brain regions involved in a coarse analysis of a stimulus. This initial coarse analysis would then influence in a top-down manner the more detailed and slower bottom-up analysis of the stimulus, operating along the occipito-temporal ventral visual stream: top-down and bottom-up flow of information would here converge ~170–180 ms (see also Price and Devlin, 2011). This complex interactive network would deal with early initial decoding of printed input and would be sensitive to contextually pre-active high-level language information.

However, early visual–orthographic EEG effects in reading have not been consistently reported, thus casting some doubts on the top-down sublexical modulation hypothesis. For example, Dehaene et al.’s (2005) proposal implies that semantic activation (such as that pre-activated in semantically constraining sentences) would not directly influence the low-level visual analysis of the stimulus. This model does not include feedback recurrent connections from semantic representations reaching the low-level sublexical analysis of a stimulus. The initial visual perceptual stages of processing would mainly send feedforward activation to build abstract orthographic word representations (Dehaene et al., 2005; Tarkiainen et al., 1999).

In the present study we will show that visual–orthographic processing is influenced by linguistic information stored in long-term memory; however, we critically provide evidence that (i) the prediction concerning the expected word must be clear-cut (as happens in specific linguistic scenarios), and that (ii) early visual word processing facilitation is incidental to neural synchronization patterns developing just before reading the expected word.

Available experimental evidence supporting the ‘top-down sublexical modulation hypothesis’ in reading is mixed. Some studies indicate that contextual semantic pre-activation needs support from lower-level representations (visual similarity of the perceived stimulus to the expected word form compared to dissimilar items) to determine early ERP effects (~130 ms, Kim and Lai, 2012). Also, when word form typicality is syntactically biased from the previous context (either expecting a noun or a verb), early increased MEG activity starting ~120 ms was recorded for the unexpected category in the occipital (visual) regions (Dikker et al.,

2010). In this study, word class typicality,¹ but not semantic knowledge, was considered as responsible for the early effect.

A series of studies (Dambacher et al., 2009; Penolazzi et al., 2007; Sereno et al., 2003), however, have reported early effects due to semantically constraining contexts that are *not* mediated by sublexical linguistic manipulations: ERP effects ~130 ms for the same word in high constraining (compared to low constraining) semantic contexts have been reported. However, these early effects depend on the lexical properties of the perceived word, being more prominent for frequent lexical items. It should be noted that frequent words represent frequent perceptual patterns habitually processed by the visual system; thus, we cannot exclude very early ERP effects for frequent words just because the visual system is more ‘trained’ in processing such frequent visual patterns.

In sum, even if some authors assume that there are no empirical constraints – in a fully interactive framework – for high-level semantic representations to interact with low-level visual–orthographic processes (Dambacher et al., 2009; Dikker et al., 2010; Kim and Lai, 2012; Sereno et al., 2003), theoretical models of visual word recognition still debate this possibility. Crucially, almost thirty years of research in this field (since the study on contextual constraint by Kutas and Hillyard, 1984) has not consistently reported expectancy-related ERP effects before 200 ms, but only effects emerging after this boundary, i.e. later than the time interval reflecting visual sublexical analyses discussed above (Barber et al., 2011; Federmeier and Kutas, 1999).² As a consequence, the available data do not fully support the *top-down sublexical modulation* hypothesis, according to which internal semantic knowledge can modulate low-level sublexical analysis of a printed word. Nonetheless, if we assume that perceptual facilitation from regions engaged in lexical/semantic processing is ‘anatomically’ possible, *why* could semantic activation not percolate down, facilitating the low-level analysis of a stimulus?³

A feasible hypothesis is that semantic contextual information does not sufficiently increase the activation levels of the expected target word (contextual pre-activation), but pre-activation would extend to a larger set of semantically related candidates (a semantic field): Federmeier and Kutas (1999) showed that a constraining sentence does not only facilitate processing of the expected word but also, to a lesser extent, of semantically related words. Among a set of semantically related candidates, one word would show a higher level of pre-activation but this pre-activation would be dispersed across the semantically related words; those semantic candidates have heterogeneous word forms (e.g. the printed stimuli ‘ant’ and ‘mosquito’ are semantically related, but not *form* related; Dikker and Pyllkanen, 2011). For this reason, contextual expectations would not condense on a single word form and the pre-activation related to the more expected item would not be high enough to top-down influence the sublexical analysis of the ‘expected’ stimulus. Following this reasoning, visual–orthographic facilitation is possible only in linguistic scenarios where contextual pre-activation is pointing toward a single lexical item.

The present study

To test the top-down sublexical modulation hypothesis (in an ecological reading situation), here we will investigate the pre-activation of two types of linguistic knowledge stored in semantic memory that

¹ The word-class distinction between nouns and verbs that shows strong orthographic form-based regularities (Farmer et al., 2006).

² It should also be noted that early effects might be short-lived or much more local than would be picked up by traditional ERP analyses of lexical/semantic violations (see Discussion in Kim and Lai, 2012). Consequently, traditional ‘N400’ studies – that employed traditional analysis strategies – may not have detected early effects.

³ EEG studies have also supported the idea that abstract letter representations are processed in occipital regions ~120 ms after stimulus presentation (Hauk et al., 2006; Tarkiainen et al., 1999).

determine different semantic contextual situations: we will compare classic semantic contexts to fixed multi-word expression contexts. Semantic memory is often described as our organized general world knowledge, in which a wide repository of information could cluster in many different ways but in at least two types of relations (Hutchison, 2003, for a review): (i) *semantic* relations, in which related items have similar meanings, because they either share specific semantic features or belong to the same semantic category, and (ii) *associative* relations, in which links between items are developed because their lexical items frequently co-occur in language. A critical distinction is that while semantic relations could be expressed based on declarative world knowledge, associative relations are well represented by recurrent experience with frequent phrasal patterns. Among lexical associations, interesting linguistic scenarios can be found in which the prediction for an incoming word is clear-cut: in corpus linguistics, a sequence of words that co-occur more often than would be expected by chance is defined as a multi-word expression and the relation between single words as ‘collocation’. Many authors (among others, Cacciari and Tabossi, 1988) have proposed that multi-word strings are represented in semantic memory as configurations of items, in which each word preserves its own lexical/semantic properties while being at the same time part of larger units. Frequent multi-word expressions provide an interesting testing ground for theories focusing on contextual pre-activation: when a multi-word expression is long enough (4–5 words), reading the initial segment could incrementally pre-activate incoming words. In other words, reading the initial part of a multi-word expression could suffice for its recognition and this, in turn, could make available the ‘missing’ lexical items (Molinaro and Carreiras, 2010; Vespignani et al., 2010). For this reason, pre-activation would be much more specific compared to the semantic pre-activation format originating from a non-fixed compositional context (as in Federmeier and Kutas, 1999).

Based on their properties, it is possible that semantic compositional and collocational highly constraining contexts (even when equated in terms of contextual predictability) could determine different expectation-related effects. In fact, while a semantic compositional context would activate a set of potential semantically-related candidates (a semantic field), a collocational context would pre-activate one specific lexical item. In the former case, activation would be dispersed across semantically-related potential candidates (as indicated by Federmeier and Kutas, 1999) that have different word forms; the more expected (activated) word would not have activation levels high enough to influence low-level perceptual processes. In the latter case, there would be no dispersion of activation, since only one candidate word would be expected (i.e. the next word of the multi-word fixed string), and such strong activation (critically related

to one single word form) could have enough power to percolate down and influence low-level visual processing.

Also, while reading a regular compositional context, each word would be incrementally integrated with the semantic information extracted from the whole sentence context and this in turn would determine probabilistic semantic estimations concerning possible following words (probabilistic pre-activation). On the other hand, collocation constraints are assumed to be a phenomenon that develops rapidly while reading the few words (4 or 5) of the multi-word string. It has been proposed (Cacciari and Tabossi, 1988; Molinaro et al., in press; Vespignani et al., 2010) that when enough incremental information concerning the multi-word string has been collected, the string would be recognized (usually in penultimate or anti-penultimate position); this, in turn would load the constellation of lexical items constituting the word string in working memory, thus making the next items already available (categorical pre-activation).

All these factors point towards more clear-cut ‘predictions’ in the collocational context, even when contextual expectations are quantitatively similar (see discussion in the following paragraph below, *Post-target word onset’ effects* section).

Post-target word onset’ effects

Previous ‘contextual expectation’ studies (Dikker et al., 2010; Kim and Lai, 2012) have mainly manipulated the target word properties (either congruent or incongruent with the context); this experimental design permits evaluation of the effect of the closure of an expectation (that would be satisfied or not) developed during the previous (typically compositional) context. In the present study, we employ a different strategy, i.e. keeping the target word constant while manipulating the properties of the context: here the context is either a high-constraining collocational context (with the target word in final position of a multi-word expression, HC-Collocation condition), or a high constraining compositional context (HC-Composition condition), or a non-constraining context (the LC-Control condition). Critically, we balanced the lexical properties of the word preceding the target across conditions and the incremental contextual predictability (measured by cloze-probability ratings), that was similar for the HC-Collocation and the HC-Composition condition (Fig. 1). These solutions are driven by the need to equate quantitative contextual differences between the two high-constraining conditions. However, conditional probability of the target word (TW) when participants were asked to report the previous word (TW-1) differed between the two HC conditions (see ‘TW if TW-1’ plots in Fig. 1). When participants reported the word preceding the target word (TW-1) of the multi word expression in the HC-Collocation condition, they also reported the expected target word (TW): this indicates that when a collocational continuation was reported

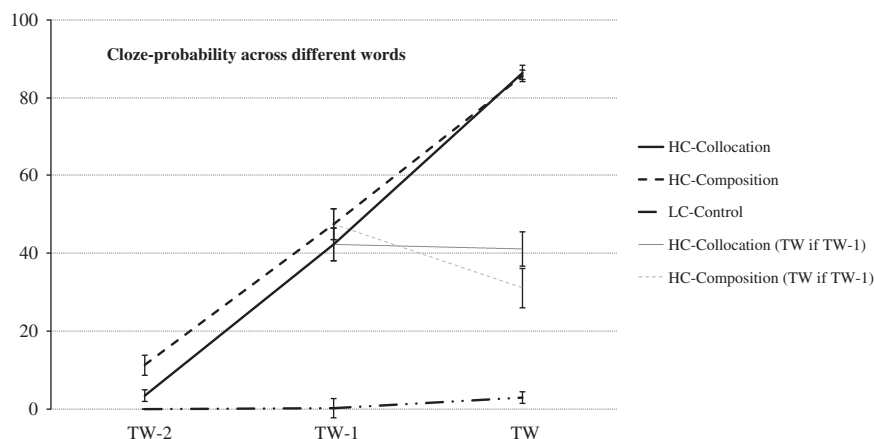


Fig. 1. Cloze-probability values (with corresponding standard error bars computed over items) for the three experimental conditions along the sentence segment of interest starting from two words before the target word (TW – 2) until the target word (TW). Conditional probability of TW when participants had to report TW-1 is also indicated (TW if TW-1).

at TW-1, there is only one possible continuation. On the other hand, when participants reported TW-1 in the HC-Compositional condition, this not involved reporting also the target word, as reflected by TW cloze-probability that dropped down: more variability of TW responses was observed across a larger set of semantically related word continuations (a semantic field). This indicates that recognition of the multi word string in the HC-Collocation condition implied expectation concerning a single possible continuation, while contextual expectation in the HC-Composition condition could extend to a larger set of word candidates.

Based on the observed conditional probability pattern, earlier ERP effects can be expected (possibly reflecting contextual facilitation ~100 ms) for the HC-Collocation condition compared to both the HC-Composition and the LC-Control conditions. The HC-Composition condition, on the other hand, should differ from the LC-Control in a later time interval. This hypothetical pattern of effects would imply that neurophysiological connections are 'available' from more high-level (semantic) representations to low-level (word form) ones. However, for semantic activation to percolate down to lower-level sublexical stages of processing, pre-activation should unambiguously 'condense' on a specific lexical item. Later effects are also expected in line with previous studies on contextual expectation both for compositional contexts (triggering a less negative effect ~400 ms in the central regions of the scalp, compared to controls; Kutas and Hillyard, 1984) and collocational contexts (triggering a positive deflection ~300 ms in the posterior areas of the scalp, compared to controls; Molinaro and Carreiras, 2010; Roehm et al., 2007; Vespignani et al., 2010).

Pre-'target word onset' effects

Kim and Lai (2012) proposed a model of rapid interaction between sub-lexical and lexical semantic representations within the first ~130 ms of visual word recognition (see also Dambacher et al., 2009; Dikker et al., 2010). According to these authors, contextual support is crucial for finding such early effects: if some internal representations are already active *before* reading the target word, we should be able to track that pre-activation during the pre-stimulus onset time interval. In addition, if different contexts (collocational vs. compositional) modulate the specificity of an expectation, this should correlate with differential effects during the pre-stimulus time interval.

Most of the ERP literature reporting expectation effects during sentence processing has focused on closure effects, i.e. on the presence/absence of changes in the expected item (post-stimulus onset). Here, we provide evidence also about sentence positions where contextual pre-activation *develops*. This is highly relevant, since how internal linguistic knowledge influences the analysis of perceptual features of a stimulus is almost an unknown territory. To provide an overall evaluation of anticipatory phenomena in reading, we will also evaluate ERP effects before the presentation of the target word: it is possible that pre-stimulus effects better explain processing facilitation of the target word.

An interesting theoretical approach to anticipatory semantics in reading was provided by Federmeier and Laszlo (2009): they proposed that integration/pre-activation phenomena reflect binding of information obtained from stimulus input with representations from short- and long-term memory (such as recent context, and accessing a word's meaning in long term memory); such binding would create meaning from the information available in the current context. From a neurophysiological perspective, Varela et al. (2001) proposed that binding phenomena would be the result of transient coupling between neuronal assemblies that are widely distributed (long-range interactions among distant brain regions). Several findings (Fries et al., 2001; Jensen and Tesche, 2002; Rodriguez et al., 2004; Weiss and Muller, 2003) suggest that brain regions that enter into synchrony are functionally involved in binding information to perform relevant cognitive tasks.

Although ERPs provide fine-grained information about the time course of cognitive events, they are not very informative about the dynamic couplings of neuronal assemblies (Bastiaansen and Hagoort, 2003). In order to quantify the coordination of activity between

neuronal assemblies, we also estimated the EEG phase-locking values (Lachaux et al., 1999): this method statistically measures the transient phase coupling between two brain signals in specific frequency bands (Varela et al., 2001). The PLV estimation is performed across trials and then averaged. After PLV calculation for each sample point available for a particular pair of signals, a time–frequency plot of PLV can then be made.

In the present study, the two high-constraining conditions were balanced for cloze-probability levels that increase right before the presentation of the word preceding the target (the word preceding the target: TW-1, ~0.42) and reach high levels for the target word (the target word: TW, ~0.85, see Fig. 1). However, different linguistic scenarios would induce dissociable expectations (as described for the TW if TW-1 cloze-probability in Post-'target word onset' effects section; see also Fig. 1 and Materials section). To evaluate such processing differences, we performed an analysis of the synchronization among the sensors in the time window presented for the previous ERP analysis: differential phase synchronization at different frequency bands and in different time intervals while reading a multi-word expressions are expected, as compared to while reading a compositional context, in particular during the preparation for the expected stimuli (i.e., during reading the pre-target word). In addition, it has been proposed that phase EEG oscillations across different frequency bands could predict the perceptual processes of a visually presented stimuli (Busch et al., 2009; VanRullen et al., 2011) suggesting that sustained attention could exert facilitation on following perceptual processes (Busch and VanRullen, 2010). We will investigate if synchronization patterns emerging before the reading of the target word (pre-TW time interval) can predict early ERP effects recorded after the target word's onset (post-TW time interval).

In sum, we here monitor both evoked and oscillatory EEG activity before and after presentation of a target word in high constraining contexts that determine differential expectations: centered on a specific lexical item (HC-Collocation) vs. related to a set of semantically-related candidates (HC-Composition). We will look for evidence of increased processing for the HC-Collocation condition compared to HC-Composition condition before reading the expected word; also, we expect earlier brain reactions for the HC-Collocation. Critically we aim at evaluating the functional relation between activity before and after the target word onset as an index of how contextual information can support fast and efficient reading.

Methods

Participants

Thirty-six native Spanish speakers (five males) took part in the experiment. They were paid 10€ per hour for their collaboration. Participants' average age was 22.9 years old (SD: 5.2). All of them

Table 1

Examples of the sentence stimuli used in the present experiment. Word preceding the target word (TW-1) is written in italics, while the target word (TW) in bold. English translation for the multi-word expression (quoted values) in the HC-Collocation condition is literal.

Condition	Example
LC-Control	Preguntó porqué tenía una venda y le expliqué que mientras cocinaba me quemé con aceite <i>la (TW-1) piel (TW)</i> de la mano. <i>He asked me why I had a bandage and I explained to her that while I was cooking I scalded the skin of my hand with oil.</i>
HC-Composition	Antes de tomar el sol es muy importante darse crema solar para proteger de quemaduras <i>la (TW-1) piel (TW)</i> del cuerpo. <i>Before sunbathing it is very important to put sunscreen on to protect the skin of the body from sunburn.</i>
HC-Collocation	No es que tenga algún problema emocional, sino que Eva tiene los sentimientos "a flor de (TW-1) piel (TW)" y por eso llora tanto. <i>Even if she does not have any emotional problem, Eva keeps her feelings "on the surface of the skin" and for this reason she cries so much.</i>

were right-handed with no history of neurological disease. Their vision was normal or corrected to normal.

Materials

Stimuli were constructed based on a set of sentences containing multi-word expressions (MWEs) that were used in a previous experiment (Molinaro and Carreiras, 2010). In that study, a set of 112 sentences containing multi-word expressions was extracted from the CESS-ECE corpus (Martí and Taulé, 2007). In this study, we adapted those sentences selecting 88 of them whose MWEs were more than 4 words long (mean: 4.05; Standard Error of the Mean, SEM: 0.10) and that showed a high number of occurrences (mean: 829.51; SEM: 215.11) in the Corpus of Referencia del Español Actual (<http://corpus.rae.es/creanet.html>). Such strings are highly familiar: a questionnaire given to 54 independent native Spanish speakers showed that such strings were rated high (5.87, SEM: 0.19) on a 7 point scale (1: never heard; 7: heard very often).

Similar to the previous study, these MWEs were inserted in sentence contexts (HC-Collocation condition, High Constraint-Collocation), trying to avoid possible pre-activations of the fixed string, or strange meanings. The target word (TW) was always in final position of the MWE, and on average in sentence position 17.40 (SD: 0.34, never in sentence final position). The target word was always a content word: 5.41 letters long on average (SEM: 0.17) with an average logFrequency of 1.69 (SEM: 0.09) and a mean number of 4.12 orthographic neighbors (SEM: 0.33).

After composing these sentences we also developed an additional 166 sentences in which the target words (TWs) were not in a collocation context, but in a non-fixed compositional context (same sentence positions, 17.40). In half of the sentences the context was semantically high-constraining (HC-Composition condition, High Constraint-Composition) and in the other half it was not constraining (LC-Control condition, Low Constraint-Control). The cloze-probability was incrementally measured by testing a group of 40 independent native Spanish speakers with an off-line questionnaire: we asked them to report the first word that most naturally continued a segment of sentence. We presented all the sentences in the three conditions until the word preceding the target (cloze-probability of TW), and until the two preceding words (cloze-probability of TW-1 and TW-2). Cloze-probability was very low on TW-2 (LC-Control: 0.00; HC-Composition: 11.32, SEM: 5.13; HC-Collocation: 3.48, SEM: 3.03); it increased on TW-1 for HC-Composition and HC-Collocation (LC-Control: 0.30; HC-Composition: 47.54, SEM: 8.01; HC-Collocation: 42.34, SEM: 8.53); on TW it was very high for HC-Composition and HC-Collocation (LC-Control: 3.12, SEM: 1.11; HC-Composition: 85.55, SEM: 3.08; HC-Collocation: 86.42, SEM: 3.56). HC-Composition and HC-Collocation sentences did not differ in their cloze-probability levels neither on TW-2 [$t(87) = 1.48$], nor on TW-1 [$t(87) = 0.75$], nor on TW [$t(87) = -0.26$]. Cloze-probability of TW, when the cloze-probability of TW-1 was considered, was the following: LC-Control: 0.00; HC-Composition: 31.12, SEM: 10.13; HC-Collocation: 41.16, SEM: 9.21; the difference between the two HC conditions was significant [$t(87) = -2.13$, $p < 0.05$]. In Fig. 1 we plot the cloze-probability for each word and condition.

We also controlled for the lexical parameters of the word preceding the target one (i.e. TW-1); this was done to avoid carry-over effects on the ERPs elicited by TW. This constituent was often a function word (LC-Control: 53; HC-Composition: 48; HC-Collocation: 52) and in the remaining cases a content word. The lexical parameters of those words across conditions were balanced (no t -value larger than 1.32) for length (LC-Control: 3.46, SEM: 0.18; HC-Composition: 3.44, SEM: 0.17; HC-Collocation: 3.22, SEM: 0.18), logFrequency (LC-Control: 1.60, SEM: 0.17; HC-Composition: 1.43, SEM: 0.15; HC-Collocation: 1.46, SEM: 0.15) and number of orthographic neighbors (LC-Control: 3.26, SEM: 0.51; HC-Composition: 2.92, SEM: 0.48; HC-Collocation: 3.32, SEM: 0.54).

The whole set of sentences (see Examples in Table 1) was constituted by 264 sentences plus an additional 12 practice sentences.

Experimental procedure

Participants were tested individually in a silent electrically-shielded room. They were seated approximately 60 cm from the CRT computer screen on which sentences were visually presented word by word (maximum visual angle: 5°) after the presentation of a fixation cross at the center of the screen for 500 ms. Words were displayed in white letters on a dark-gray background. Each word was presented for 300 ms followed by a 300-ms blank screen, the inter-trial interval was variable (500–1700 ms). Sentence order was fully randomized and every five sentences on average, participants were asked to answer a YES/NO comprehension question by pressing the corresponding button on a joystick; comprehension questions appeared randomly across the whole experiment. YES/NO button position appeared randomly on the either on the left (half of the times) or on the right (half of the times). Participants across the experiments showed a very good average level of accuracy (95.2%), varying between 83% and 98%.

To familiarize participants with the experimental procedure, before the experimental session participants had to perform 12 practice trials in the presence of the experimenter. The experiment lasted 1 h and 15 min, with a break every 15 min.

EEG data acquisition

EEG was recorded through a BrainAmp system with 32 channels. Twenty-eight Ag/AgCl electrodes were arranged on an EasyCap recording cap based on the 10–10 International System. Additional external electrodes of the same material were placed on mastoids A1, A2 and around eyes left Veog, right Veog, left Heog and right Heog. Monopolar differential recording was on-line referenced to the left mastoid. Impedance was kept below 5 k Ω for mastoid and scalp electrodes, and below 10 k Ω for EOG electrodes. Data were acquired at a sampling rate of 500 Hz.

ERP analysis

EEG was band-pass filtered off-line (0.1–30 Hz) and re-referenced to the average activity of the two mastoids. The recordings were then segmented in time-intervals between –100 and 1400 ms time-locked to the presentation of TW-1: this interval included a time window until 800 ms post TW presentation. Epochs were visually inspected to exclude other possible artifactual effects in the ERP analyses: 5.49% of epochs were rejected on average (no across-condition differences). After baseline correction (–100, 0 ms), epochs were averaged independently for each participant, electrode and condition: single-subject ERPs were then grand-averaged for visual inspection. It should be noted that an ERP analysis time-locked to TW was also performed considering time intervals from –100 to 800 ms and baseline correction (–100, 0 ms). ERP effects elicited by the TW reading were very similar in the ERP analysis time-locked to TW-1 and that time-locked to TW. We here present the analysis time-locked to TW-1 since it is the more conservative and it is the one used for the synchrony analysis described below.

Statistical analysis performed on time intervals of interest was done using two separate strategies. The *Midline* analysis was employed to evaluate activity in the dorsal electrodes: a two-way Analysis of Variance considered Longitude (three levels: Fz, Cz, Pz) and Condition (three levels: LC, HC-Composition and HC-Collocation) as main factors. The *Distributed* analysis considered ERP activity across groups of electrodes: Left Anterior (LA: average activity of Fp1, F3, F7, FC1), Right Anterior (RA: Fp2, F4, F8, FC2), Left Central (LC: FC5, T7, C3, CP1), Right Central (RC: FC6, T8, C4, CP2), Left Posterior (LP: O1, P3, P7, CP5), Right Posterior (RP: O2, P4, P8, CP6). A three-way ANOVA considered Longitude (three levels: Anterior, Central, Posterior), Hemisphere (two levels: Left, Right) and Condition as main factors. Overall effects of Condition were then explored via pairwise comparisons between

the three conditions using similar strategies and topographies for the analysis. Probability values were Greenhouse–Geisser corrected when needed. To better detect the source of an interaction between a topographical factor and the experimental manipulation, post-hoc comparisons (FDR corrected) were planned for each electrode (*Midline analyses*) or Group (*Distributed analysis*).

Phase synchrony method

Raw EEG signal was first segmented into a series of epochs lasting 2800 ms including 1800 ms preceding the TW. Electrodes placed near the eyes were excluded from the analysis in order to avoid biological artifacts. The continuous 50 Hz (AC) component was filtered in each epoch with a zero-phase filter that keeps the biological 50 Hz signal. Then the filtered signal was convolved with a complex Gabor wavelet (7 cycles) through trials and subjects for each condition. By this process we obtained the signal phase for frequencies between 1 and 90 Hz with 1 Hz frequency resolution. Phase information was then used to compute the PLV. This method involves computing the phase difference in a time window for an electrode pair and assessing the stability of such phase difference through all trials. If Φ_i and Φ_j are unitary vectors representing the phase of EEG signals in electrodes *i* and *j*, phase differences are represented by unitary vectors obtained by:

$$\Phi_{ij} = \Phi_i \text{conj}(\Phi_j)$$

The PLV is the length of the vector resulting from the vector sum of difference vectors through the trials (with the sum operating throughout all of the trials), where *N* is the number of trials:

$$PLV_{ij} = \text{abs}(\sum \Phi_{ij}) / N$$

The PLV index ranges from 0 to 1, with value 1 indicating perfect synchronization (phase difference is perfectly constant throughout the trials) and value 0 representing total absence of synchrony (phase differences are random). Phase synchronization across the entire trial for each frequency bin was normalized to a baseline 800 ms preceding TW-1 onset. The normalized signal (*S_N*) was obtained by subtracting the average activity of the baseline (μ) from the filtered signal (*S*) divided by the standard deviation of the baseline (σ), in a frequency by frequency manner:

$$S_N = (S - \mu) / \sigma$$

Because we were interested in long-range coordination of neural activity, we included all electrode pairs in the calculation to produce a global index of synchronization across a large frequency range. The statistical analyses of the phase synchrony were performed on all time–frequency charts resulting from averaging the electrophysiological responses of all electrode pairs during the entire segment (–1800 to 1000 ms after TW onset). This resulted in a grand average time–frequency plot per experimental condition per subject. Those plots were then grouped by condition and analyzed by means of a permutation test in search of statistically significant differences between them (Burgess and Gruzelier, 1999). In the permutation test, the time–frequency plots belonging to different conditions are mixed to compute a random distribution. This is then used to evaluate the statistical significance of the results. The permutation test assumes that the ‘real’ differences between conditions should exceed the random differences. The α level was set at 0.05.

The permutation procedure detected significant differences across condition in four time–frequency windows (TFWin effect) ($p < 0.05$). We found two TFWin effects before the onset of TW (*THETA pre-TW effect* and *GAMMA pre-TW effect*, see below), and other two after the onset of TW (*GAMMA post-TW_a effect* and *GAMMA post-TW_b effect*, see below).

Table 2

Results of the overall ANOVA considering the three conditions in the earlier time intervals. Bold values indicate significant effects. Acronyms in the Factors column indicate the following: C indicates the Condition factor, L indicates Longitude and H indicates Hemisphere (see *Methods* section). Between brackets we indicate the degrees of freedom (d.f.).

Time interval	Analysis	Factors (d.f.)	MSE	F
100–130 ms	<i>Midline</i>	C (2,68)	3.58	3.75*
		C × L (4,136)	0.32	0.10
	<i>Distributed</i>	C (2,68)	3.30	4.75*
		C × L (4,136)	0.48	0.39
		C × H (2,68)	0.38	1.07
200–240 ms	<i>Midline</i>	C × L × H (4,136)	0.07	0.20
		C (2,68)	4.07	1.34
	<i>Distributed</i>	C × L (4,136)	0.46	2.92*
		C (2,68)	3.65	1.48
		C × L (4,136)	0.63	4.49*
		C × H (2,68)	0.51	0.11
		C × L × H (4,136)	0.06	0.09

* $p < 0.05$.

The mean PLV, over the time–frequency window identified, across all electrode pairs per experimental condition, was entered in a repeated measure ANOVA with Condition (three levels: LC, HC-Composition and HC-Collocation) and TFWin effect (four levels: *THETA pre-TW effect*, *GAMMA pre-TW*, *GAMMA post-TW_a* and *GAMMA post-TW_b*) as within-subjects factors. In this ANOVA, PLV differences are demonstrated by a significant Condition by TFWin effect interaction (see *Results* section).

For the topographical analysis of phase synchronization, we restricted our analysis to the TFWin effects previously selected. We averaged the TFWin effect independently for each electrode pair: this resulted in arrays of electrode pairs, for each experimental condition, per subject. Those arrays were then analyzed by means of paired t-test ($p < 0.05$) that contrasted HC-Collocation and HC-Composition versus LC. False Discovery Rate ($q < 0.002$) was used to correct for multiple comparisons in each one of the entry matrix of p-values (Benjamini and Yekutieli, 2001).

Correlation analysis

We also aimed at better establishing the relation between the synchrony patterns observed in the pre-TW time interval and the ERP effects we recorded in the post-TW epoch (see *Results* sections). This analysis was suggested by previous reports indicating that phase EEG oscillations could predict effectiveness in the perceptual analysis of a visually-presented stimuli (Busch et al., 2009; VanRullen et al., 2011). We calculated for each participant one single PLV value that represented the average value of the 5% most active connections (Table 3) for the PLV pre-TW effect for each HC condition; we then subtracted the result for the LC-Control condition from the HC condition values for each participant to determine the increased phase synchronization. Those values were correlated with the ERP effects emerging for the HC conditions minus LC-Control for each electrode and participant. We then obtained a correlation value for each electrode that was employed to calculate a correlation map between pre-TW increased phase synchronization and each post-TW ERP effects (see Fig. 4).

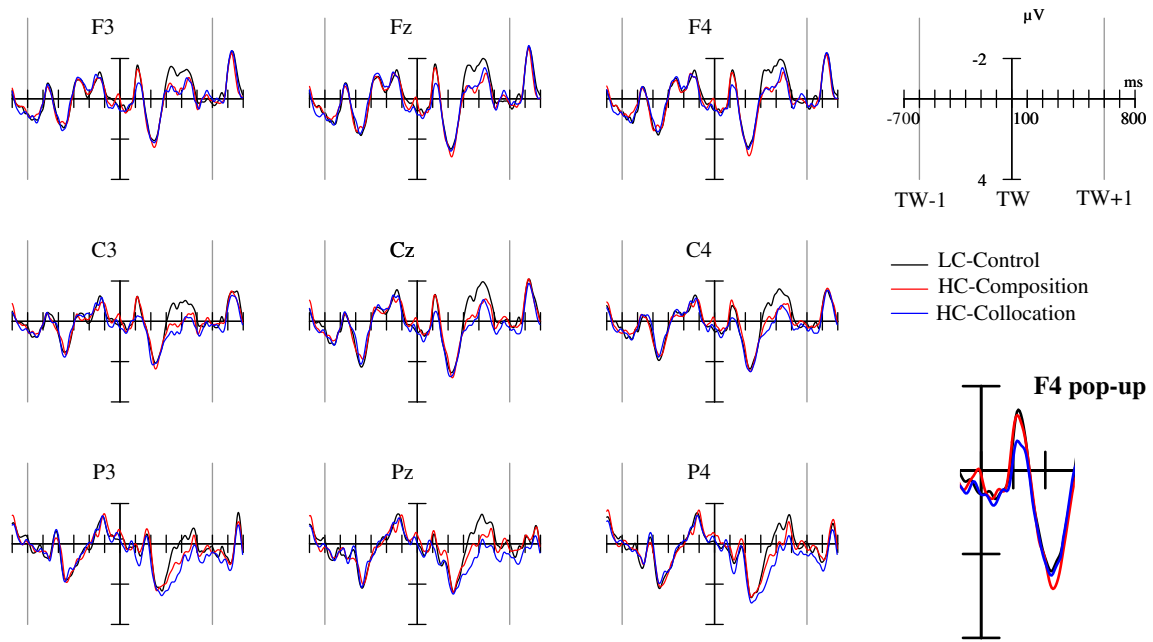
Results

ERPs

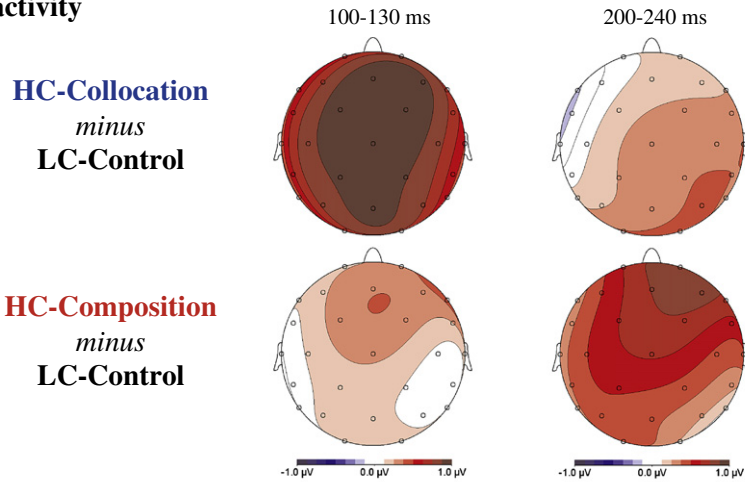
Fig. 2 shows the ERP data time-locked to the presentation of the word preceding the target (TW-1).

Early ERP effects

No effect is evident until the presentation of the target word (TW) at 600 ms. Around 120 ms after TW onset a positive effect is evident for



Early ERP activity



Late ERP activity

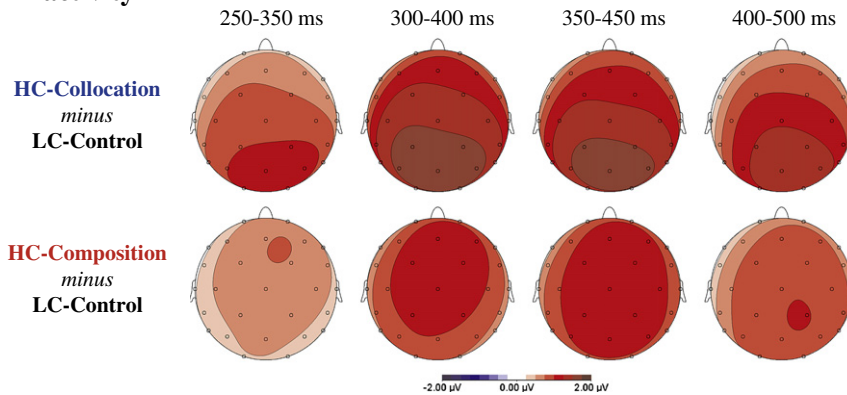


Fig. 2. Upper panel: event related potentials (ERPs) elicited time-locked to the reading of the word preceding the target (TW-1) until 800 ms post-target word (TW) onset for each experimental condition. On the right we report a detail of the early ERP effects time-locked to TW in the electrode F4. Negative voltages are plotted up. Lower panel: voltage maps of the ERPs elicited by the TW in the two high-constraining conditions minus the low-constraining condition. We distinguish the distribution of the earlier effects from the later ERP effects (distinguished in time-windows of 100 ms shifting for 50 ms in time).

the HC-Collocation condition compared to the other two conditions; the effect is distributed all over the scalp, but larger in the frontal regions, thus resembling an N1 effect. After this effect, a more positive peak

~200 ms (identifiable as a P2 effect) is evident in the frontal regions of the scalp for the HC-Composition condition compared to the other two conditions (Fig. 2).

We quantified the earlier effect as the mean voltage in the time interval between 100 and 130 ms, i.e. a time interval centered around peak-activity. A Main effect of Condition emerged in the overall analysis (Table 2). The pairwise comparison between HC-Collocation and LC-Control showed a main effect of Condition [Midline: $F(1,35) = 6.02$, $MSE = 3.83$, $p < 0.05$; Distributed: $F(1,35) = 7.19$, $MSE = 3.68$, $p < 0.01$]. The same effect of Condition emerged in the contrast between HC-Collocation and HC-Composition [Midline: $F(1,35) = 4.49$, $MSE = 3.58$, $p < 0.05$; Distributed: $F(1,35) = 5.93$, $MSE = 3.38$, $p < 0.05$]. No relevant effects emerged in the HC-Composition vs. LC-Control contrast.

The later effect was quantified in the time interval between 200 and 240 ms (time interval centered around peak-activity, see Table 2). The pairwise comparisons showed significant interactions between Condition and Longitude for the HC-Composition condition compared to the LC-Control condition [Distributed: $F(2,70) = 4.25$, $MSE = 0.72$, $p < 0.01$]: after grouping electrode regions per Longitude (Anterior, Central and Posterior), a significant effect emerged in the Anterior group [$t(35) = -2.49$, $p_{FDRcorr} < 0.05$]. The HC-Composition vs. HC-Collocation revealed the same interaction between Condition and Longitude [Distributed: $F(2,70) = 7.29$, $MSE = 0.54$, $p < 0.05$]: following the same strategy used for the previous contrast a significant effect emerged on the Anterior group [$t(35) = -2.42$, $p_{FDRcorr} < 0.05$]. No differences emerged for the HC-Collocation vs. LC-Control analysis.

Late ERP effects

Around 250 ms the HC-Collocation condition started differing from the other two conditions in the posterior regions. On the other hand, the HC-Composition condition differed from the LC-Control later in time (~300 ms). The two High Constraint conditions differed from the LC-Control condition all over the scalp but the effect was larger for the HC-Collocation condition in posterior regions of the scalp. Around 500 ms the two HC conditions showed similar effects (Fig. 2).

This last effect was evaluated in the 250–500 ms time interval, a canonical time interval used in the N400 literature. The overall ANOVA showed a main effect of Condition [Midline: $F(2,70) = 10.64$, $MSE = 3.94$, $p < 0.001$; Distributed: $F(2,70) = 8.55$, $MSE = 4.48$, $p < 0.001$] and interaction between Condition and Longitude [Midline: $F(4,140) = 6.83$, $MSE = 0.43$, $p < 0.01$; Distributed: $F(4,140) = 5.40$, $MSE = 4.05$, $p < 0.01$].

The HC-Collocation vs. LC-Control contrast elicited a main effect of Condition [Midline: $F(1,35) = 9.58$, $MSE = 4.56$, $p < 0.001$; Distributed: $F(1,35) = 12.16$, $MSE = 4.81$, $p < 0.001$] and the interaction between Condition and Longitude [Midline: $F(2,70) = 8.47$, $MSE = 0.47$, $p < 0.001$; Distributed: $F(2,70) = 8.21$, $MSE = 0.68$, $p < 0.001$]. These last interactions were mainly due the larger effect in posterior regions [Midline: $Pz: t(35) = -3.97$, $p_{FDRcorr} < 0.001$; Distributed: Posterior: $t(35) = -4.41$, $p_{FDRcorr} < 0.001$].

On the other hand, the HC-Composition vs. LC-Control only elicited a main effect of Condition [Midline: $F(1,35) = 12.59$, $MSE = 3.51$, $p < 0.001$; Distributed: $F(1,35) = 14.15$, $MSE = 3.37$, $p < 0.001$].

Interestingly, the HC-Collocation vs. HC-Composition contrast also showed the interaction between Condition and Longitude [Distributed: $F(2,70) = 6.23$, $MSE = 0.66$, $p < 0.001$]. This interaction is mainly due to the effect in the Posterior electrodes [$t(35) = -4.12$, $p_{FDRcorr} < 0.05$]. However, when splitting this time interval into small time windows of 100 ms shifting in time for 50 ms (250–350 ms; 300–400 ms; 350–450 ms; 400–500 ms) the interaction was not significant in the late time interval [Midline: $F(2,70) = 2.45$, $MSE = 0.42$, *n.s.*; Distributed: $F(2,70) = 1.95$, $MSE = 0.76$, *n.s.*]. We thus performed an ad-hoc three-way ANOVA considering Longitude (three-levels collapsing the Hemisphere factor: Anterior, Central, Posterior), Time Window (two levels: 250–350 ms, 400–500 ms) and Condition (two levels: HC-Collocation, HC-Composition). This analysis was designed to evaluate possible dissociations between the ERPs elicited by the two High Constraint conditions. In this analysis the interactions between Condition and Longitude

[$F(2,70) = 15.14$, $MSE = 0.42$, $p < 0.001$] and among Condition, Longitude and Time Window [$F(2,70) = 3.85$, $MSE = 0.09$, $p < 0.05$] emerged. This last interaction thus indicates that qualitatively different processes are operating in the two time intervals.

Summary of ERP results

No ERP effects emerged time-locked to the word preceding the target (Fig. 2). After TW onset an early (~120 ms) widely distributed effect emerged for the HC-Collocation condition compared to the other two conditions. This effect does not seem a carry-over from the previous word but emerges time-locked to the presentation of the target word. Given the more prominent frontal scalp distribution, we consider it as reflecting a reduced N1 for the HC-Collocation condition. In a later time interval (~220 ms) the HC-Composition condition differed from the other two conditions, eliciting a larger P2.

Later in time (after 250 ms), the two High Constraint condition elicited robust less negative amplitudes compared to the Low Constraint condition. However, while the effect for the HC-Composition condition was distributed all over the scalp, the effect for the HC-Collocation condition was mainly posterior: in these scalp regions ERP amplitudes were more positive for the HC-Collocation condition compared to the HC-Composition in the earlier time interval (250–350 ms), while they did not differ in the later time interval (400–500 ms). These differences supported previous findings that dissociated between distinct neurocognitive processes (Molinaro and Carreiras, 2010; Vespignani et al., 2010) in the time interval (250–500 ms) classically considered as reflecting a unitary process termed N400.

Critically, using a different experimental design compared to our previous studies – where the target word is constant across conditions – revealed early differential ERP effects that we have not reported before.

Phase synchrony

The results are illustrated in Fig. 3A.

PLV results

The significant interaction between Condition and Frequency emerged [$F(2,70) = 4.887$, $MSE = 0.840$; $p < 0.0002$] confirming that phase synchrony was different across conditions. Specifically, for HC-Collocation condition, we identified a significant increase of THETA phase synchrony (5–6 Hz), from –320 ms to –120 ms

Table 3

5% electrode pairs showing higher PLV values in the analysis of synchrony in the pre-TW time interval in the high constraining conditions. The HC-Collocation condition showed increased synchrony in the –320 to –120 ms time interval in the Theta band; the HC-Composition condition showed increased synchrony in the –440 to –360 ms time interval in the Gamma band.

HC-Collocation Theta synchrony			HC-Composition Gamma synchrony		
Electrode A	Electrode B	PLV	Electrode A	Electrode B	PLV
O1	P4	0.754	O1	F4	0.474
FZ	O1	0.740	PZ	O1	0.446
FC2	FP2	0.718	O1	P3	0.430
CP6	O1	0.698	PZ	FZ	0.397
CZ	P3	0.678	P7	FP1	0.392
FZ	O2	0.667	PZ	P7	0.391
O2	F3	0.655	FZ	O1	0.361
CP6	O2	0.628	FC5	FP1	0.360
FC5	FZ	0.613	FC6	FP1	0.353
FC6	FP1	0.606	FZ	P3	0.342
F4	F3	0.594	FC6	FZ	0.333
O1	FP1	0.591	P7	F4	0.331
P4	F4	0.581	O1	FP1	0.320
CP6	F4	0.579	FZ	F4	0.318
P8	P4	0.575	T7	C4	0.309
T7	FP2	0.532	CP5	C4	0.304
FZ	P4	0.529	FC2	FZ	0.304

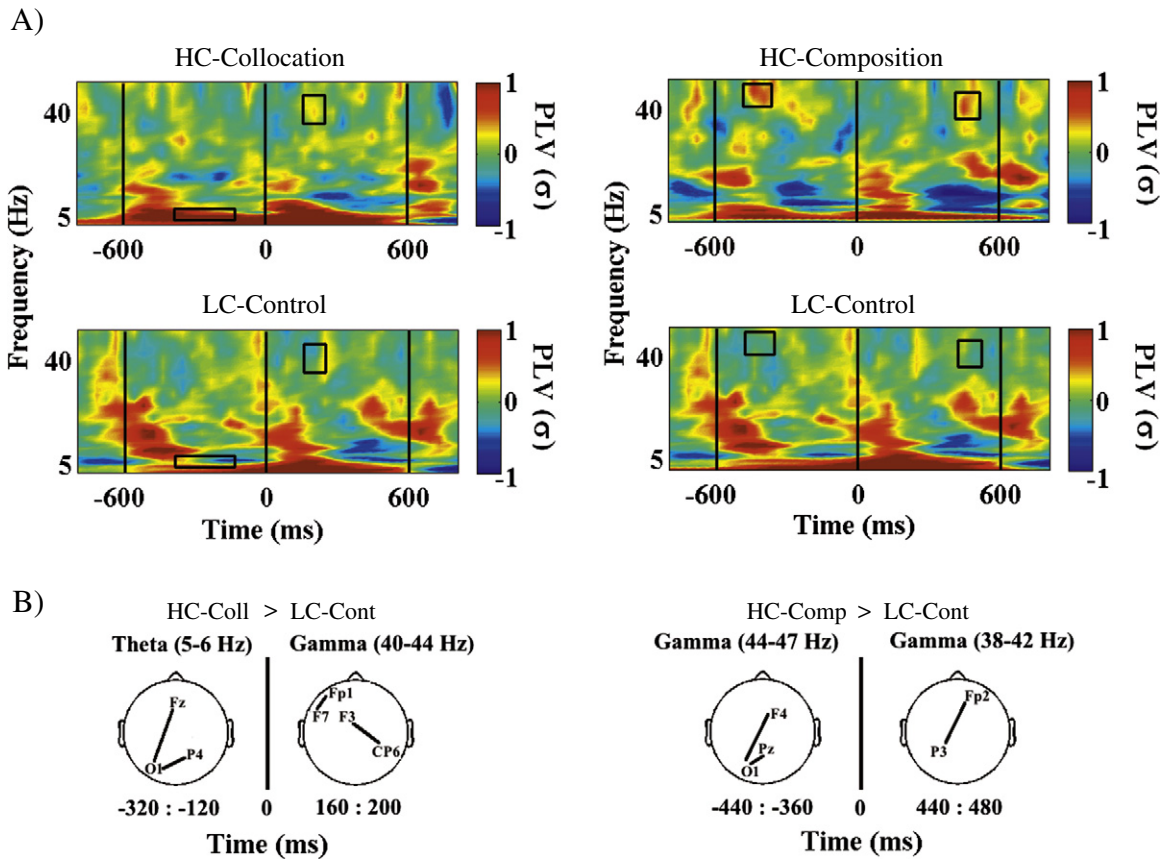


Fig. 3. Phase synchrony charts and scalp topography. (A) The time–frequency maps per experimental condition. Experimental conditions are indicated at the top of the maps. Frequency range and time are indicated in the y and x axis of the maps respectively. Color bars at the right side of the maps show the magnitude of the phase-locking value (in standard deviation units). Vertical lines indicate the onset of TW-1, TW and TW + 1 respectively. The black rectangles in the maps indicate the time–frequency intervals that are significantly different between conditions [$p < 0.05$]. (B) Topographical significant differences of phase synchrony between experimental conditions. Experimental conditions compared are indicated at the top of the scalps. Oscillation frequency and temporal window are indicated at the top and bottom of each scalp respectively. Time 0 indicates the onset of the TW. Black lines connect pairs of electrodes displaying significantly larger synchronization [$p_{FDRcorr} < 0.002$].

preceding the onset of the TW, and of GAMMA phase synchrony (40–44 Hz), from 160 ms to 200 ms after the onset of the TW, compared to the LC-Control condition [$\text{THETA pre-TW: } F(1,35) = 10.877$, $\text{MSE} = 4.128$, $p < 0.002$; $\text{GAMMA post-TW: } F(1,35) = 5.722$, $\text{MSE} = 0.030$, $p = 0.022$] and to the HC-Composition condition [$\text{THETA pre-TW: } F(1,35) = 4.611$, $\text{MSE} = 6.241$, $p < 0.039$; $\text{GAMMA post-TW: } F(1,35) = 4.267$, $\text{MSE} = 0.024$, $p = 0.046$]. Also, for HC-Composition condition, we observed an increase of GAMMA phase synchrony (44–47 Hz), from –440 ms to –360 ms preceding the onset of the TW, and of GAMMA phase synchrony (38–42 Hz), from 440 ms to 480 ms after the onset of the TW, compared to the LC-Control condition [$\text{GAMMA pre-TW: } F(1,35) = 8.667$, $\text{MSE} = 0.833$, $p < 0.006$; $\text{GAMMA post-TW: } F(1,35) = 7.613$, $\text{MSE} = 0.037$, $p = 0.009$] and to the HC-Collocation [$\text{GAMMA pre-TW: } F(1,35) = 13.933$, $\text{MSE} = 0.623$, $p < 0.001$; $\text{GAMMA post-TW: } F(1,35) = 8.790$, $\text{MSE} = 0.034$, $p < 0.005$].

Topography of the connectivity patterns is illustrated in Fig. 3B. Compared to LC-Control condition, HC-Collocation strongly increased THETA phase synchrony over Fz-O1 [$t(35) = 3.33$, $p_{FDRcorr} < 0.002$] and P4-O1 [$t(35) = 3.21$, $p_{FDRcorr} < 0.002$] sites, 320 ms before to onset of the TW, and enhanced GAMMA phase synchrony over Fp1-F7 [$t(35) = 3.25$, $p_{FDRcorr} < 0.002$] and F3-CP6 [$t(35) = 3.48$, $p_{FDRcorr} < 0.002$] sites, 160 ms after to onset to the TW. In contrast, HC-Composition, also compared to LC, increased GAMMA phase synchrony among F4-O1 [$t(35) = 4.21$, $p_{FDRcorr} < 0.002$] and Pz-O1 [$t(35) = 3.59$, $p_{FDRcorr} < 0.002$] sites, 440 ms before to onset of the TW, and enhanced GAMMA phase synchrony among Fp2-P3 [$t(35) = 3.20$, $p_{FDRcorr} < 0.002$] sites, 440 ms after to onset to the TW.

Correlation analyses

We considered the following possible correlations: (i) with respect to the processing of the HC-Collocation condition we focused on the relation between increased THETA synchrony in the pre-TW interval (THETA pre-TW) and both the reduced 100–130 ms effect and the later 250–500 ms effect recorded in the post-TW interval (effects calculated subtracting the LC-Control condition from HC-Collocation); (ii) with respect to the processing of the HC-Composition condition we focused on the relation between increased GAMMA synchrony in the pre-TW interval (GAMMA pre-TW) and both the increased 200–240 ms effect and the later 250–500 ms effect recorded in the post-TW interval (effects calculated subtracting the LC-Control condition from HC-Composition).

Across the four correlation maps (Fig. 4), significant values emerged for the correlation between THETA pre-TW increased synchronization and the early (100–130 ms) ERP effect (Pearson correlation coefficient, two-tailed probability $p < 0.01$), especially in frontal (electrode F4: $r = 0.51$, $p < 0.01$; FC6: $r = 0.46$, $p < 0.01$) and occipital (O2: $r = 0.44$, $p < 0.01$) regions of the scalp. Among all the other correlation maps, no significant effects emerged (no r values larger than ± 0.3).

Discussion

The main findings of the present experiment can be summarized as follows. High constraining contexts influence the processing of a target word from very early moments of low-level processing: the collocational contexts of multi-word expressions elicit very early (~120 ms) brain

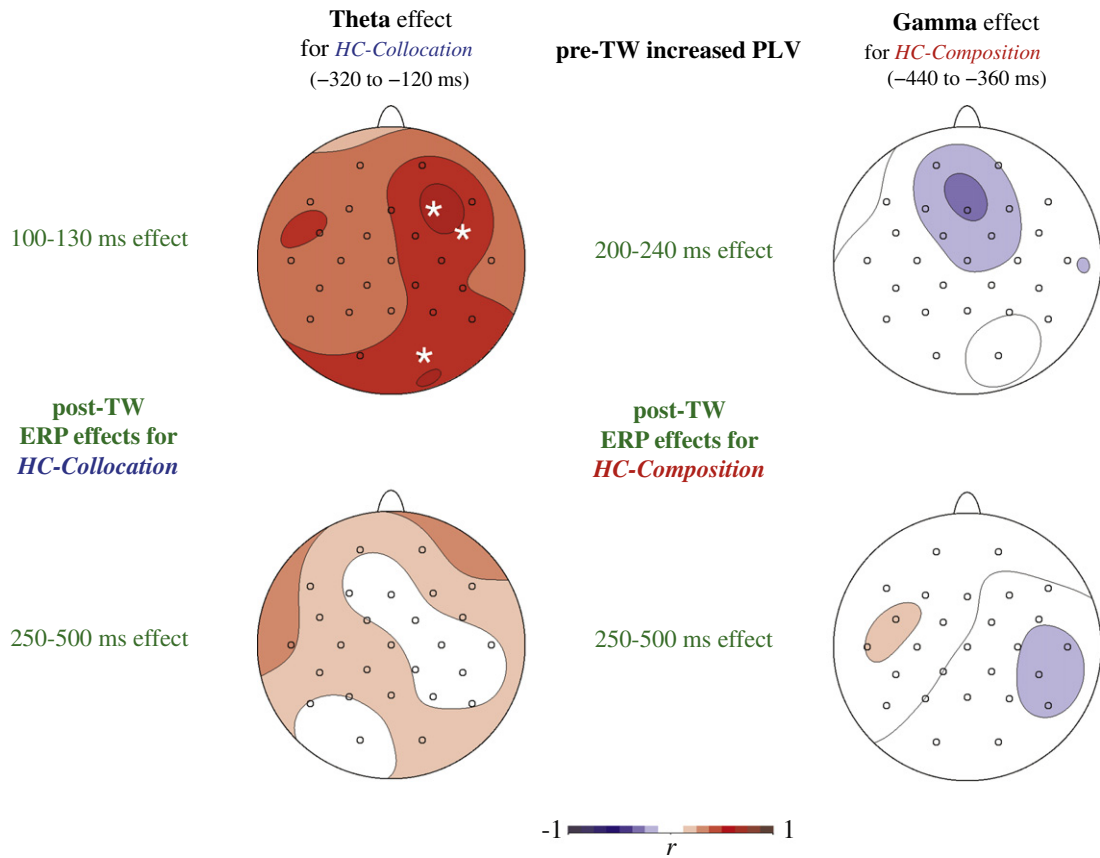


Fig. 4. Correlation maps reflecting Pearson correlation coefficients (–1 to 1) both between increased pre-TW Theta synchronization for the HC-Collocation condition and post-TW ERP voltage differences (HC-Collocation minus LC-Control) in specific time intervals of interest for each electrode (left maps) and between increased pre-TW Gamma synchronization for the HC-Composition condition and post-TW ERP voltage difference (HC-Composition minus LC-Control) in specific time intervals of interest for each electrode (right maps). Significant correlations are indicated by white asterisks.

reactions compared to compositional contexts, influencing the more basic sublexical processing of the expected word. Differential synchronization effects for collocational (in the theta band) and compositional (in the gamma band) constructions emerged before reading the target word: increased theta synchronization correlated with the initial visual–orthographic analysis of the target word in collocational contexts.

Early visual-attentional facilitation

Very few studies have found evidence for contextual facilitation during word reading at the low-level sublexical processing stages (Dambacher et al., 2009; Dikker et al., 2009, 2010; Kim and Lai, 2012; Penolazzi et al., 2007; Sereno et al., 2003). Such findings are consistent with eye movement results showing contextual effects within 200 ms after target word reading (Sereno and Rayner, 2003) and could be accommodated within a neural framework of fast and efficient reading.

However, experimental evidence supporting the idea that linguistic knowledge could interact with basic perceptual processes is mixed. Some theoretical proposals (Dehaene et al., 2005) suggest that computations in posterior cortical regions would mainly involve feedforward spread of activation that builds up abstract orthographic representations: such processes would not be influenced by internal linguistic knowledge stored in long-term memory. Similarly, Lau et al. (2008) propose that brain activity related to word-level representations could only emerge after 200 ms post-stimulus (see also Kutas and Federmeier, 2011).

Previous studies using high constraining contexts have all involved compositional word-by-word incremental processes. In the present study, the earliest effect for compositional contexts was reported as

modulating the frontal P2 component (~220 ms). P2 effects for word recognition have already been reported in a variety of tasks: as an example, a priming experiment by Misra and Holcomb (2003) reported an enhanced P2 for targets that were immediate repetitions of their primes. In the sentence comprehension literature, recent studies have shown that the P2 is more positive for strongly constrained sentence endings (Barber et al., 2011; Federmeier and Kutas, 1999) and especially for right (compared to left) visual field presentations (thus implying that attentional resources are modulated by left-hemisphere brain regions: Federmeier et al., 2005; Wlotko and Federmeier, 2007). Here we bring additional evidence for increased P2 for high constraining compositional contexts. This component has been classically considered as reflecting visual processes under attentional control (Luck, 2005) with decreased positivity for items that require increasing attention. An expected word in a high constraining compositional context will be more easily classified (receive contextual top-down pre-activation) compared to a low-constraining context, thus requiring less visual attentional resources to be recognized.

More importantly, we report earlier effects (~120 ms) for the reading of words in high constraining collocation contexts: the N1 showed a reduced effect for 'collocational' expected words as compared to the same item in the compositional context. When spatial location of a stimulus is kept constant, N1 effects are assumed to reflect discriminative visual processing of a specific stimulus (Vogel and Luck, 2000). The present findings thus support the idea that feedback activation could percolate down to the low-level form-related processing of the stimulus that could, in turn, be modulated by expectations developed while reading the previous context. This observation fits with recent findings reported by Madec et al. (2012) that showed significant correlation between item-level ERPs at right occipital sites around 100 ms and letter

identification times in the corresponding behavioral task. This supports the hypothesis that the early effect we observed for the HC-Collocation condition reflects easier visual–orthographic processes during sentence reading.

Compared to previous studies that reported similar early effects for mismatching stimuli (Dikker et al., 2009, 2010; Kim and Lai, 2012) or reports in which such early effects strongly depend on the stimulus properties (Dambacher et al., 2009; Penolazzi et al., 2007) we show that similar effects can be obtained while manipulating the context and using *exactly* the same stimulus across conditions. We propose that when contextual pre-activation consolidates on a single lexical item without dispersing on semantically related items, word recognition is facilitated from its lowest level processing stages. Similar conclusions were reached by studies using a picture-noun matching task: early perceptual facilitation emerged only when a single lexical item could be predicted (Dikker and Pylkkanen, 2011, *in press*). Even so, how does such contextual pre-activation emerge?

Increased phase synchronization before TW reading

We were able to dissociate between pre-activations developed during reading the previous context by maintaining constant the level of expectation as measured by cloze-probability ratings. As evident in Fig. 1, similar increases of expectation precede the target word; nonetheless, conditional probability of TW depending on TW-1 reports shows that the two HC contexts differ in the type of expectation they determine: the compositional context pre-activates a semantic field that incrementally constrains semantic expectations toward a specific word (but also to related items), while a collocational context depends on the retrieval of a familiar configuration of words from long-term memory (Configuration Hypothesis, Cacciari and Tabossi, 1988). These two processes have been well differentiated through the synchronization patterns recorded before the target word presentation.

- A. While reading the non-fixed compositional context we observed increased gamma synchronization ~200 ms after reading the word preceding the target (TW-1) and ~450 ms after reading the target word (TW). Even if the effect was detected at slightly different frequencies, it could be argued that the same process is at work while reading the words where semantic expectations increase. That the effect is earlier for TW-1 and slightly later for the TW could be related to the fact that the word preceding the target was in most cases a function closed-class word, i.e. an item that is not conveying the same amount of lexical/semantic meaning as a content open-class word (TW was always a content word). Previous research has already reported increased gamma power for expected items in high-constraining contexts (Hald et al., 2006), which has been interpreted as the successful matching 'between the pre-activation of the neural representation of the predicted word, and the neural representation of the actually incoming word' (Wang et al., 2012, page 11). In this framework, semantic binding (Federmeier and Laszlo, 2009) could reflect successful mapping of the physical properties of an external stimulus onto a corresponding internal neural representation (Revonsuo, 1999; Varela et al., 2001).
- B. While reading the collocational context, we observed a long-lasting increase of theta synchronization after reading the word preceding the target (starting ~100 ms until 500 ms after the onset of TW-1) and an increased gamma effect ~180 ms after reading the target word (TW). Theta oscillation was initially proposed to reflect a mechanism that mediates a dynamic link between hippocampus and neocortical areas that process long-term memory traces (Miller, 1991). Sentence-related reports also suggest that theta oscillations could reflect working memory operations (Bastiaansen et al., 2002; but see also Jensen and

Tesche, 2002). In the present experiment, we considered the word preceding the target word in multi-word expressions as the position where the fixed expression is recognized (recognition point; Cacciari and Tabossi, 1988; Vespignani et al., 2010). The recognition of a multi-word expression implies the retrieval of the configuration of words from long-term memory, thus determining increased working memory load (Configuration Hypothesis: Cacciari and Tabossi, 1988). Once the multi-word string is recognized, expectation concerning the following words (and specifically TW) develops, which determines the post-TW increased gamma synchronization recorded for this condition.

In the oscillatory phase domain, the main finding is that synchronization across different frequency bands was detected for the two high-constraining conditions before reading the target word (in the absence of an ERP effect). The most interesting aspect in both cases is that the strongest coupling was recorded between frontal and occipital electrodes, thus suggesting that we are tapping here into some preparatory processes before reading a highly expected word: frontal regions are possibly communicating with occipital brain regions to anticipate some features of the next incoming stimulus.

Relation between pre-TW phase synchronization and post-TW visual-attentional processes

Some proposals indicate that EEG oscillations are good predictors of visual perceptual processes (Busch et al., 2009; Dikker and Pylkkanen, *in press*; VanRullen et al., 2011). We investigated if there was a direct relation between the evoked ERP effects recorded in the earlier post-TW time intervals and the increased synchronization patterns before TW onset. This is relevant since it could better constrain the scalp regions in which evoked activity is modulated by an earlier process. This analysis revealed that the N1 effect (largely distributed over the scalp) for the TW in the collocational conditions correlated well across participants with the increased theta synchronization observed time-locked to the preceding word. This suggests that the more robust the working memory load triggered by the multi-word configuration, the more effective is the early facilitation in the perceptual analysis of the next incoming words. This effect probably reflects some inter-individual variability in the familiarity with multi-word expressions: the more familiar a participant is with a multi-word expression, the stronger the pre-activation of the next word; this, in turns determines facilitation in the visual perceptual analysis of the following items of the string.

The correlation between theta synchronization and early evoked activity (N1 effect) was stronger in the frontal and the occipital regions. Previous research indicated that mapping visual features onto abstract orthographic representation elicited a component with very similar scalp topography (in masked priming paradigms, N/P150, Grainger and Holcomb, 2009) thus suggesting that facilitatory processes are dealing with sublexical form-related neural representations. It is interesting to note that a frontal–occipital (slightly right-lateralized) correlation pattern emerged – similar to the theta topographical pattern emerging for theta synchronization: it could be argued that the early facilitatory effect recorded ~120 ms post-TW onset for the collocation condition could reflect neural coupling between frontal and occipital brain regions along the dorsal visual pathway (due to earlier theta phase synchronization). More anatomical fine-grained measures (such as MEG) can potentially resolve this issue in next future. Dikker and Pylkkanen (*in press*) have already reported interesting MEG findings using a picture-word matching paradigm. They reported enhanced activity in the theta band in the visual, left temporal, and ventro-medial prefrontal cortex before stimulus onset (interpreted as reflecting contextual pre-activation) plus they found prediction-congruity effects after stimulus onset in the same regions. This set of data nicely converge with our findings; differently from Dikker and Pylkkanen, we employed

ecological stimuli where words were embedded in sentence contexts (while they used a picture-word matching paradigm); in addition, we statistically prove the correlation between pre-stimulus and post-stimulus effects (between frontal and occipital sites), while they mainly inferred that pre-activation effects and post-stimulus effects are related. Thus, our study and the picture-word matching study provide complementary evidence (from different experimental paradigms) of the neural mechanism supporting anticipation effects in language.

We did not observe significant correlation between the P2 effect and the preceding increased gamma-activity for the high-constraining compositional condition. Gamma-activity here reflects the matching between the bottom-up processing of the printed word and the internal neural representation of the expected word (as suggested by Wang et al., 2012), but not the development of expectations per se. Also, the P2 is not reflecting visual perceptual discrimination of a stimulus, but the recruitment of higher-level attentional resources required for following higher-order cognitive processes. For such reasons the two phenomena could be somewhat related but not necessary inter-dependent.

Later ERP effects

Later ERP effects, after 250 ms, deserve a special mention. Previous research on contextual constraint has mainly focused on the inverse relation between cloze-probability and the negative amplitude of the N400 component (Kutas and Hillyard, 1984). Such ERP modulation has been classically suggested to reflect a unitary component reflecting lexical/semantic processing of a target word (Lau et al., 2008). Research on multi-word expressions (Molinaro and Carreiras, 2010; Roehm et al., 2007; Vespignani et al., 2010), however, has reported qualitatively different modulations within the 250–500 ms time interval: an initial phase (related with a positive peak emerging ~300–350 ms) was shown to be mainly related to contextual expectations, while a later phase (reflected by the negative deflection peaking ~400 ms) was suggested to reflect more integrative semantic processes.

In this paper, we directly compared two qualitatively different high-constraining contexts (collocational vs. compositional) that elicit different expectations concerning the target word. In line with previous proposals, we found different effects developing in an earlier time interval (250–350 ms), while they become similar later (400–500 ms). In addition, the collocational condition elicited a more posterior scalp effect, compared to the compositional condition that elicited a more central scalp effect.

The early dissociation (250–350 ms) supports the notion that in the two conditions the pre-activated information is different: more focused pre-activation concerning a single lexical item in the collocational condition and more sparse pre-activation across semantically related items in the compositional condition. Instead of creating new labels for those different ERP phenomena, we (Vespignani et al., 2010) based the functional interpretation of these two processes on an attentional model proposed by Kok (2001) that distinguishes between different types of expectations: a more categorical pre-activation of internal representations (eliciting the so-called P300 component, in a time interval corresponding to consolidation of whole-word orthographic representations, Grainger and Holcomb, 2009) and a more probabilistic one (eliciting a partially overlapping negative effect, see discussion in Vespignani et al., 2010). Different timing in the gamma synchronization was reported after TW onset for the two high constraining conditions: the effect was much earlier for the collocation condition (~180 ms) compared to the composition condition (after 400 ms). Based on the proposal that gamma-band activity would reflect contextual expectancy (Wang et al., 2012), this indicates that different expectancy-related effects emerged for the presentation of the same item in different contexts, with the one emerging in the collocation condition earlier in time.

These results support the view that the 200–600 ms ERP time interval (heuristically labeled N400, Kutas and Federmeier, 2011) is reflecting brain activity in which higher-level processes related to

contextual expectation (either probabilistic or categorical) and semantic combinatory (Molinaro et al., 2010, 2012) continuously interact, giving rise to the observed ERP modulations in this time interval.

A framework for anticipatory effects in sentence reading

In this study we were able to show that the initial low-level processing of a stimulus can be facilitated by the pre-activation elicited by the previous context (in line with the *top-down sublexical modulation* hypothesis). In the *compositional* context a set of potential word candidates are activated before reading the expected word. Among them, one candidate is more 'expected' than the others; however, its activation is not high enough (since other items are competing). Multiple word forms are possible and there is no commitment for one of them. This implies higher attentional demands when TW is read (correlating with the P2 effect). In the *collocational* context only one possible candidate is pre-activated and its activation is not competing with any other item. This determines higher activation levels for TW compared to compositional context and top-down support for the sublexical word form analysis of the expected item (correlating with the N1 effect).

The contextually pre-activated information is critical for developing unambiguous predictions of the low-level visual features of a printed word. Pre-stimulus phase synchronization patterns suggest that such contextual pre-activation could drive and mediate word recognition processes at multiple levels of processing. Based on a model for object recognition proposed by Bar et al. (2006), we propose that anticipation phenomena in sentence reading strongly depend on long-distance connections between frontal and posterior brain regions. Bar et al. proposed that low-detailed representations of a visual stimulus are available in frontal regions of the brain already ~130 ms; such activation would then converge with more detailed processing along the ventral visual pathways to construct a fine-grained representation of the visual stimulus (see Dell'Acqua et al., 2010, for similar findings with a picture-word paradigm). Here, we show that contextual information can stimulate this frontal-posterior connectivity even before the target word reading: anticipatory long-lasting theta frequency coupling along the frontal-posterior dimension is required to facilitate visual-orthographic processing of the expected word. However, if contextual pre-activation is not focused on a specific word (and its form), only correlating with anticipatory short-lived gamma coupling along the frontal-posterior axis, additional feedforward activation from perceptual levels of processing to higher-level processing stages is needed. This, in turn, determines processing facilitation along the word recognition workflow later in time (after 200 ms).

Conclusions

Overall, these results provide critical support for a model in which recurrent neural connections at work during a pre-stimulus time interval play a critical active role in supporting post-stimulus onset feedforward neural activity elicited by an external alphabetic stimulus.

Acknowledgments

This research has been partially supported by Grants PSI2012-32350, PSI2009-08889/PSIC and CONSOLIDER-INGENIO2010 CSD2008-00048 from the Spanish Government and ERC-2011-ADG-295362 grant from the European Research Council. NM was partially supported by a 'Juan de la Cierva' grant from the Spanish Government. PB was supported by the associative research program CONICYT, Project CIE-05. We thank Eugenio Rodriguez and Mario Chavez for providing analysis tools and Margaret Gillon-Dowens for her comments. We are especially grateful to Cristina Cacciari for constructive discussions about multi-word expressions and to two anonymous reviewers for the enlightening review process.

References

- Bar, M., Kassam, K.S., Ghunam, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., Hamalainen, M.S., Marinkovic, K., Schacter, D.L., Rosen, B.R., Halgren, E., 2006. Top-down facilitation of visual recognition. *PNAS U.S.A.* 103, 449–454.
- Barber, H.A., Ben-Zvi, S., Bentin, S., Kutas, M., 2011. Parafoveal perception during sentence reading? An ERP paradigm using rapid serial visual presentation (RSVP) with flankers. *Psychophysiology* 48, 523–531.
- Bastiaansen, M.C.M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. *Cortex* 39, 967–972.
- Bastiaansen, M.C.M., van Berkum, J.J., Hagoort, P., 2002. Event-related theta power increases in the human EEG during online sentence processing. *Neurosci. Lett.* 323, 13–16.
- Benjamini, Y., Yekutieli, D., 2001. The control of the false discovery rate in multiple testing under dependency. *Ann. Stat.* 29, 1165–1188.
- Bernal, B., Altman, N., 2010. The connectivity of the superior longitudinal fasciculus: a tractography DTI study. *Magn. Reson. Imaging* 28, 217–225.
- Burgess, A.P., Gruzeliier, J.H., 1999. Methodological advances in the analysis of event-related desynchronization data: reliability and robust analysis. In: Pfurtscheller, G., Lopes da Silva, F.H. (Eds.), *Handbook of Electroencephalography & Clinical Neurophysiology*, 6. Elsevier, Amsterdam, The Netherlands, pp. 139–160.
- Busch, N.A., VanRullen, R., 2010. Spontaneous EEG oscillations reveal periodic sampling of visual attention. *PNAS U.S.A.* 107, 16048–16053.
- Busch, N.A., Dubois, J., VanRullen, R., 2009. The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci.* 29, 7869–7876.
- Cacciari, C., Tabossi, P., 1988. The comprehension of idioms. *J. Mem. Lang.* 27, 668–683.
- Connolly, J.F., Phillips, N.A., 1994. Event-related potential components reflect phonological and semantic processing of the terminal word of spoken sentences. *J. Cogn. Neurosci.* 6, 256–266.
- Cornelissen, P.L., Kringelbach, M.L., Ellis, A.W., Whitney, C., Holliday, I.E., Hansen, P.C., 2009. Activation of the left inferior frontal gyrus in the first 200 ms of reading: Evidence from magnetoencephalography (MEG). *PLoS One* 4, e5359.
- Dambacher, M., Rolf, M., Göllner, K., Kiegl, R., Jacobs, A.M., 2009. Event-related potentials reveal rapid verification of predicted visual input. *PLoS One* 4, e5047.
- Dehaene, S., Cohen, L., Sigman, M., Vinckier, F., 2005. The neural code for written words: a proposal. *Trends Cogn. Sci.* 9, 335–341.
- Dell'Acqua, R., Sessa, P., Peressotti, F., Mulatti, C., Navarrete, E., Grainger, J., 2010. ERP evidence for ultra-fast semantic processing in the picture–word interference paradigm. *Front. Psychol.* 1, 177.
- Dikker, S., Pyllkanen, L., 2011. Before the N400: effects of lexical–semantic violations in visual cortex. *Brain Lang.* 118, 23–28.
- Dikker, S., Pyllkanen, L., in press. Predicting language: MEG evidence for lexical preactivation. *Brain Lang.* <http://www.sciencedirect.com/science/article/pii/S0093934X12001587>.
- Dikker, S., Rabagliati, H., Pyllkanen, M., 2009. Sensitivity to syntax in visual cortex. *Cognition* 110, 293–321.
- Dikker, S., Rabagliati, H., Farmer, T.A., Pyllkanen, L., 2010. Early occipital sensitivity to syntactic category is based on form typicality. *Psychol. Sci.* 21, 629–634.
- Farmer, T.A., Christiansen, M.H., Monaghan, P., 2006. Phonological typicality influences on-line sentence comprehension. *PNAS U.S.A.* 103, 12203–12208.
- Federmeier, K.D., Kutas, M., 1999. A rose by any other name: long-term memory structure and sentence processing. *J. Mem. Lang.* 41, 469–495.
- Federmeier, K.D., Kutas, M., 2001. Meaning and modality: influences of context, semantic memory organization, and perceptual predictability on picture processing. *J. Exp. Psychol.: Learn. Mem. Cogn.* 27, 202–224.
- Federmeier, K.D., Laszlo, S., 2009. Time for meaning: Electrophysiology provides insights into the dynamics of representation and processing in semantic memory. In: Ross, B.H. (Ed.), *Psychology of Learning and Motivation*, 51. Academic Press, Burlington, MA, pp. 1–44.
- Federmeier, K.D., Mai, H., Kutas, M., 2005. Both sides get the point: hemispheric sensitivities to sentential constraint. *Mem. Cogn.* 33, 871–886.
- Fries, P., Reynolds, J.H., Rorie, A.E., Desimone, R., 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291, 1560–1563.
- Grainger, J., Holcomb, P.J., 2009. Watching the word go by: on the time-course of component processes in visual word recognition. *Lang. Linguist. Compass* 3, 128–156.
- Hald, L.A., Bastiaansen, M.C.M., Hagoort, P., 2006. EEG theta and gamma responses to semantic violations in online sentence processing. *Brain Lang.* 96, 90–105.
- Hauk, O., Davis, M.H., Ford, M., Pulvermüller, F., Marslen-Wilson, W.D., 2006. The time course of visual word recognition as revealed by linear regression analysis of ERP data. *NeuroImage* 30, 1383–1400.
- Hutchison, K.A., 2003. Is semantic priming due to association strength or feature overlap? A microanalytic review. *Psychon. Bull. Rev.* 10, 785–813.
- Jensen, O., Tesche, C.D., 2002. Frontal theta activity in humans increases with memory load in a working memory task. *Eur. J. Neurosci.* 15, 1395–1399.
- Kim, A., Lai, V., 2012. Rapid interactions between lexical–semantic and word-form analysis during word recognition in context: evidence from ERPs. *J. Cogn. Neurosci.* 24, 1104–1112.
- Kok, A., 2001. On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology* 38, 557–577.
- Kutas, M., Federmeier, K.D., 2000. Electrophysiology reveals semantic memory use in language comprehension. *Trends Cogn. Sci.* 4, 463–470.
- Kutas, M., Federmeier, K.D., 2011. Thirty years and counting: finding meaning in the N400 component of the event related potentials (ERP). *Annu. Rev. Psychol.* 62, 621–647.
- Kutas, M., Hillyard, S.A., 1984. Brain potentials during reading reflect word expectancy and semantic association. *Nature* 307, 161–163.
- Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J., 1999. Measuring phase synchrony in brain signals. *Hum. Brain Mapp.* 8, 194–208.
- Lamme, V.A., Roelfsema, P.R., 2000. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579.
- Lau, E.F., Phillips, C., Poeppel, D., 2008. A cortical network for semantics: (de)constructing the N400. *Nat. Rev. Neurosci.* 9, 920–933.
- Luck, S.J., 2005. *An introduction to the Event-Related Potential technique*. MIT Press, Cambridge, MA.
- Maded, S., Rey, A., Dufau, S., Klein, M., Grainger, J., 2012. The time course of visual letter perception. *J. Cogn. Neurosci.* 24, 1645–1655.
- Martí, M.A., Taulé, M., 2007. CESS-ECE: Corpus anotados del español y catalán. *Arena Romanística. Corpus and text linguistics Romance studies*, 1. Department of Foreign Languages, Bergen, Norway.
- McClelland, J.L., Rumelhart, D.E., 1981. An interactive activation model of context effects in letter perception: Part 1. An account of basic findings. *Psychol. Rev.* 88, 375–407.
- Miller, R., 1991. *Cortico-hippocampal interplay and the representation of contexts in the brain*. Springer-Verlag, Berlin.
- Misra, M., Holcomb, P.J., 2003. Event-related potential indices of masked repetition priming. *Psychophysiology* 40, 115–130.
- Molinaro, N., Carreiras, M., 2010. Electrophysiological evidence of interaction between contextual expectation and semantic integration during the processing of collocations. *Biol. Psychol.* 83, 176–190.
- Molinaro, N., Conrad, M., Barber, H.A., Carreiras, M., 2010. On the functional nature of the N400: contrasting effects related to visual word recognition and contextual semantic integration. *Cogn. Neurosci.* 1, 1–7.
- Molinaro, N., Carreiras, M., Duñabeitia, J.A., 2012. Semantic combinatorial processing of non-anomalous expressions. *NeuroImage* 59, 3488–3501.
- Molinaro, N., Canal, P., Vespignani, F., Pesciarelli, F., Cacciari, C., in press. Are complex function words processed as semantically empty strings? A reading time and ERP study of Collocational Complex Prepositions. *Lang. Cogn. Process.* <http://dx.doi.org/10.1080/01690965.2012.665465>.
- Pammer, K., Hansen, P.C., Kringelbach, M.L., Holliday, I., Barnes, G., Hillebrand, A., Singh, K.D., Cornelissen, P.L., 2004. Visual word recognition: the first half second. *NeuroImage* 22, 1819–1825.
- Penolazzi, B., Hauk, O., Pulvermüller, F., 2007. Early semantic context integration and lexical access as revealed by event-related brain potentials. *Biol. Psychol.* 74, 374–388.
- Price, C.J., Devlin, J.T., 2011. The Interactive Account of ventral occipitotemporal contributions to reading. *Trends Cogn. Sci.* 15, 246–253.
- Revonsuo, A., 1999. Binding and the phenomenal unit of consciousness. *Conscious. Cogn.* 8, 173–185.
- Rodríguez, R., Kallenbach, U., Singer, W., Munk, M.H., 2004. Short- and long-term effects of cholinergic modulation on gamma oscillations and response synchronization in the visual cortex. *J. Neurosci.* 24, 10369–10378.
- Roehm, D., Bornkessel-Schlewiesky, I., Roesler, F., Schlewiesky, M., 2007. To predict or not to predict: influences of task and strategy on the processing of semantic relations. *J. Cogn. Neurosci.* 19, 1259–1274.
- Sereno, S.C., Rayner, K., 2003. Measuring word recognition in reading: eye movements and event-related potentials. *Trends Cogn. Sci.* 7, 489–493.
- Sereno, S.C., Brewer, C.C., O'Donnell, P.J., 2003. Context effects in word recognition: evidence for early interactive processing. *Psychol. Sci.* 14, 328–333.
- Tarkiainen, A., Helenius, P., Hansen, P.C., Cornelissen, P.L., Salmelin, R., 1999. Dynamics of letter string perception in the human occipitotemporal cortex. *Brain* 122, 2119–2132.
- VanRullen, R., Busch, N.A., Dreves, J., Dubois, J., 2011. Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Front. Psychol.* 2, 60.
- Varela, F., Lachaux, J.P., Rodriguez, E., Martinerie, J., 2001. The Brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2, 229–239.
- Vespignani, F., Canal, P., Molinaro, N., Fonda, S., Cacciari, C., 2010. Predictive mechanisms in idiom comprehension. *J. Cogn. Neurosci.* 22, 1682–1700.
- Vogel, E.K., Luck, S.J., 2000. The visual N1 component as an index of a discrimination process. *Psychophysiology* 37, 190–203.
- Wakana, S., Jiang, H., Nagae-Poetscher, L.M., van Zijl, P.C.M., Mori, S., 2004. Fiber tract-based atlas of human white matter anatomy. *Radiology* 230, 77–87.
- Wang, L., Zhu, Z., Bastiaansen, M.C.M., 2012. Integration or predictability? A further specification of the functional role of gamma oscillations in language comprehension. *Front. Psychol.* 3, 1–12.
- Weiss, S., Müller, H.M., 2003. The contribution of EEG coherence to the investigation of language. *Brain Lang.* 85, 325–343.
- Wlotko, E.W., Federmeier, K.D., 2007. Finding the right word: hemispheric asymmetries in the use of sentence context information. *Neuropsychologia* 45, 3001–3014.