



Dissociating the pre-activation of word meaning and form during sentence comprehension: Evidence from EEG representational similarity analysis

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Accepted: 10 September 2023
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Abstract

During language comprehension, the processing of each incoming word is facilitated in proportion to its predictability. Here, we asked whether anticipated upcoming linguistic information is actually *pre-activated* before new bottom-up input becomes available, and if so, whether this pre-activation is limited to the level of semantic features, or whether extends to representations of individual word-forms (orthography/phonology). We carried out Representational Similarity Analysis on EEG data while participants read highly constraining sentences. Prior to the onset of the expected target words, sentence pairs predicting semantically related words (*financial* “bank” – “loan”) and form-related words (*financial* “bank” – *river* “bank”) produced more similar neural patterns than pairs predicting unrelated words (“bank” – “lesson”). This provides direct neural evidence for item-specific semantic and form predictive pre-activation. Moreover, the semantic pre-activation effect preceded the form pre-activation effect, suggesting that top-down pre-activation is propagated from higher to lower levels of the linguistic hierarchy over time.

Keywords Prediction · Pre-activation · Form · Meaning · Homograph · Hierarchy

Introduction

Prediction plays a vital role in language comprehension, as it allows us to process language more quickly and accurately (Kuperberg & Jaeger, 2016). However, there is ongoing debate regarding the nature of these predictions, and the levels of representation at which they are generated (Kuperberg & Jaeger, 2016). There is a growing consensus that we use prior contexts to pre-activate the *meanings* of upcoming words. For example, given the context “*I went to deposit the check at the...*”, we are likely to predict the semantic features of the expected word, “bank” (e.g., <financial> and <service>), which will facilitate the processing of “bank” if it is subsequently encountered (Federmeier & Kutas,

1999; Kutas & Federmeier, 2011). A far more contentious issue is whether we additionally pre-activate the linguistic *form* of anticipated words. For example, do we additionally pre-activate the orthographic representation, /B-A-N-K/, before this information actually becomes available from the bottom-up input? Addressing this question is crucial, as it would offer valuable insights into the computational principles and mechanisms of predictive language processing, and the nature of predictive processing more generally.

One possibility is that we only predict at the semantic level. For example, during incremental language comprehension, the evolving representation of the prior context may interact or “resonate” with words stored in long-term semantic memory (e.g. Gerrig & McKoon, 1998; Myers & O'Brien, 1998; Van Berkum, 2009), or with higher-level representations of common events or states, which may passively spread activation to associated semantic features of upcoming words (Paczynski & Kuperberg, 2012; Sanford et al., 2011; for discussion, see Kuperberg et al., 2011; Lau et al., 2013).

An alternative theory, grounded in hierarchical generative frameworks (Kuperberg & Jaeger, 2016, Section 5), such as predictive coding (Mumford, 1992; Rao & Ballard, 1999), proposes that predictions are propagated down from higher

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to lower levels of the representational hierarchy over time. On this account, the highest-level ongoing interpretation of the prior context actively propagates predictions downward to pre-activate upcoming lexico-semantic information (the semantic features associated with upcoming words), which, in turn, propagate predictions further down to pre-activate specific upcoming word-form representations at the level of orthography/phonology.

Thus far, existing studies have not been able to distinguish between these accounts. Some studies using event-related potentials (ERPs) have reported effects of predictability on early ERP components that are linked to the processing of word-forms (Brothers et al., 2015; Connolly & Phillips, 1994; Federmeier et al., 2005; Groppe et al., 2010; Lau et al., 2013), while others have reported an attenuation of the N400, a measure of lexico-semantic predictability, in response to unexpected words that are orthographically related to anticipated words (DeLong et al., 2019, 2021; Ito et al., 2016; Laszlo & Federmeier, 2009). ERP effects have also been reported on pre-target words that are incongruous with the form-level features of upcoming expected words, such as “an” versus “a” when the context strongly constrains for the expected word, “kite” (DeLong et al., 2005). However, several of these results have proved difficult to replicate (e.g., Nieuwland et al., 2018), and others may not offer unequivocal evidence of word-form pre-activation (for a review, see Nieuwland, 2019). Most importantly, because ERPs index neural activity that is time-locked to the onset of new input, they assess the *effects* of prediction on bottom-up processing, rather than directly isolating predictive activity itself.

To circumvent this issue, some researchers have examined oscillatory activity *before* the onset of predictable *versus* unpredictable words. There have been some reports of effects that localize to lower-level cortical regions, which have been interpreted as reflecting anticipatory activity at the level of orthography (Wang et al., 2018a) or even low-level visual features (Dikker & Pylkkänen, 2013). Others, however, have argued that these effects reflect pre-stimulus differences in attention or arousal, rather than prediction *per se* (Terporten et al., 2019).

In the present study, we took a different approach. We employed Representational Similarity Analysis (RSA) to ask whether the brain generates distinct neural patterns that correspond to the pre-activation of the meaning (e.g., <financial> and <service>) and the form (i.e., orthography and phonology; e.g., /B-A-N-K/ and /bæŋk/) of specific upcoming words before this information became available from the bottom-up input. The basic assumption of RSA is that representationally similar items produce patterns of neural activity that are more similar to each other than representationally distinct items (Kriegeskorte et al., 2008). When used in conjunction with time-sensitive neurophysiological methods, like EEG or MEG, RSA can also tell us *when*

this representationally specific information becomes active (Cichy et al., 2014; Stokes, 2015).

In a recent MEG study (Wang et al., 2018b), we used RSA to show that, during sentence comprehension, the patterns of neural activity produced before the appearance of upcoming words were more similar when pairs of contexts predicted the same words (e.g., “baby” – “baby”) than when they predicted different words (e.g., “baby” – “rose”). This provided evidence that item-specific information associated with upcoming words was pre-activated before the bottom-up input actually appeared. However, it was unclear whether comprehenders only pre-activated the semantic features of upcoming words (e.g., <little>, <cute>, <crying>), or whether predictions were additionally generated at the level of word-form (e.g., /B-A-B-Y/, /'berbi/).

To address this question directly, we implemented a novel experimental design that aimed to dissociate the pre-activation of meaning and form. We developed triplets of highly constraining sentence contexts that gave rise to two types of *related* sentence pairs. First, *semantically-related* pairs constrained for upcoming words that shared meaning but not form (e.g., “I went to deposit the check at the... [bank]” and “His college was very expensive, so he had to take out a student... [loan]”). Second, *form-related* pairs constrained for homographs that shared form but not meaning (e.g., “I went to deposit the check at the... [bank]” and “The muddy sides of the river are called the river... [bank]”).¹ Across triplets, *unrelated* sentence pairs constrained for words that shared neither meaning nor form, and therefore served as a control condition (e.g., “I went to deposit the check at the... [bank]” and “After waking up, the student went to his first... [class]”).

We measured EEG as participants silently read these sentences for comprehension. At each time point from the onset of the pre-target word until the onset of the predicted target word, we computed the similarity between the spatiotemporal patterns of neural activity produced by each type of sentence pair. If readers pre-activate the *semantics* of upcoming words, then the neural patterns produced by the *semantically related* pairs should be significantly more similar than the patterns produced by the *unrelated* pairs.

¹ In line with all accounts of predictive language comprehension, and all theories of post-onset homograph processing, we assume that in highly constraining contexts, the appropriate meaning of the homograph is pre-activated. For example, the dominant financial-related meaning of the word “bank” should be pre-activated following a dominant-constraining context, while the subordinate river-related meaning of the word “bank” should be pre-activated following the subordinate-constraining context. In the psycholinguistic literature, there has been some debate about whether, *after* a homograph is encountered from bottom-up input, we additionally access its contextually-inappropriate meaning. Addressing this question is outside the scope of the present study.

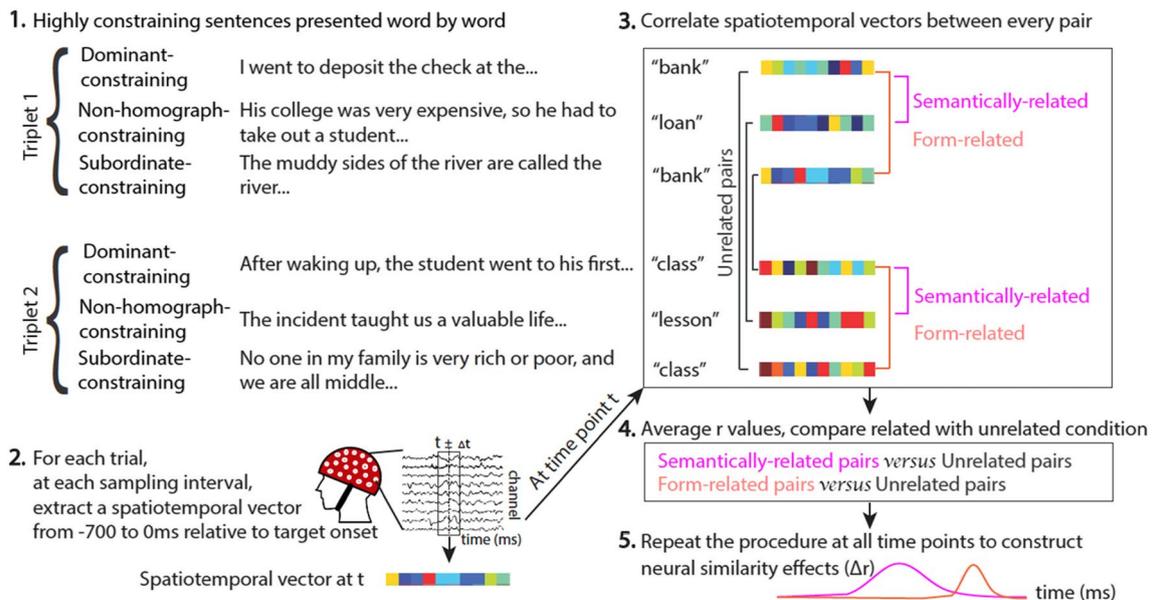


Fig. 1 Schematic illustration of our representational similarity analysis stream. **1.** Participants read triplets of highly constraining sentences (pseudorandomly presented). **2.** For each trial, and at the center of each sampling interval ($t \pm \Delta t$) within our time window of interest (from -700 to 0 ms relative to the target onset), we extracted a vector of EEG data that represented the spatiotemporal pattern of activity produced across all EEG channels. **3.** We calculated Pearson's r between each pair of spatiotemporal vectors to quantify the neural similarity between the patterns of EEG activity produced by predicted upcoming words in (a) *semantically related* pairs where the predicted words shared semantic but not form features, (b) *form-*

related homograph pairs where the predicted words shared form but not semantic features, and (c) *unrelated* pairs where the predicted words shared neither form nor semantic features. **4.** To isolate item-specific semantic and form similarity effects, we averaged the r values separately for the *semantically related* and *form-related* pairs, and statistically compared them with the patterns produced by the *unrelated* pairs. **5.** We subtracted the average neural similarity values of the *unrelated* pairs from those of *semantically related* and *form-related* pairs (Δr) at each sampling point to construct time series of the *semantic* and *word-form* pre-activation effects

If readers additionally pre-activate the *form* of upcoming words, then the patterns produced by the *form-related* pairs should be significantly more similar than those produced by the *unrelated* pairs. Finally, if top-down predictions are propagated from higher to lower levels of the representation over time, then the semantic pre-activation effect should precede the form pre-activation effect.

Methods

Design and development of stimuli

Experimental design

We constructed 84 triplets of highly constraining sentences that each predicted a specific upcoming word (Fig. 1A). The contexts within each triplet were distinct from one another, and they had no content words in common. Each triplet was comprised of three types of sentence contexts: (1) dominant-constraining contexts that predicted the dominant meaning of a homograph (e.g., the *financial* meaning of “bank”), (2) non-homograph-constraining contexts that predicted a word

that was semantically related to the dominant meaning of the homograph (e.g., “loan”), and (3) subordinate-constraining contexts that predicted the same homograph's subordinate meaning (e.g., the *river* meaning of “bank”). This yielded two types of sentence pairs within each triplet: *semantically-related* pairs ($n = 84$), in which the predicted words were associated in meaning but not in form (e.g., *financial* “bank” – “loan”), and *form-related* pairs ($n = 84$), in which the predicted homographs overlapped in form but not in meaning (e.g., *river* “bank” – *financial* “bank”). Across different triplets, there were 31,374 *unrelated* sentence pairs, in which the predicted words were always distinct in both form and meaning (“loan” – “lesson”; “bank” – “class”, etc.). This large number of *unrelated* pairs served as a control condition.

To construct these stimuli, we carried out a series of cloze norming tests (Taylor, 1953). Native English speakers, recruited through Amazon Mechanical Turk, read the sentence contexts without the target words (e.g., “I went to deposit the check at the...”) and completed each sentence by writing down the first word that came to mind. Items were counterbalanced across lists to ensure that each participant observed only one item from each triplet. After three rounds

of cloze norming, responses for each item were obtained from an average of 39 participants (range: 33–48). Based on these norms, we selected the final set of 84 sentence triplets in which at least 67% of participants provided the expected target word across all three sentences (mean lexical constraint = 88%, SD = 8%).

In the EEG experiment, participants saw all three types of sentence contexts within each triplet (dominant-constraining, non-homograph-constraining, and subordinate-constraining), pseudorandomized and separated by at least 30 trials (mean separation = 69 trials). To avoid repeating the same homograph twice within an experimental session, half of the dominant-constraining contexts and half of the subordinate-constraining contexts ended with the expected homographs, and the other half ended with another plausible but unexpected completion that was never provided in the cloze norming study (0% cloze). This excluded the possibility that, instead of directly reflecting representational activity related to form pre-activation itself, any form similarity effect reflected participants' recognition of a match between the form of the word that they had just predicted and a homograph that they had seen earlier in the experiment. The pairing of contexts with the expected and unexpected endings was counterbalanced across two experimental lists, ensuring that each participant saw an equal number of dominant-constraining and subordinate-constraining contexts that ended with expected and unexpected words. Because the non-homograph-constraining contexts always ended with the expected word (88% cloze), two thirds of all sentences in the experimental session ended with expected words.

Characterization of stimuli

Semantic similarity between pairs of predicted target words

Our design rested on the assumption that the predicted words in the *semantically related* pairs were more semantically related to each other than in the *unrelated* pairs. To confirm that this was the case, we quantified the semantic similarity between the pairs of predicted word using WordNet from the Natural Language Toolkit (NLTK) (Loper & Bird, 2002). WordNet is an English lexical database that organizes words based on their semantic relations in a hierarchical network, such as their super-subordinate relations (e.g., “meal” – “breakfast”) and part-whole relations (e.g., “sand” – “beach”). Unlike other tools for measuring semantic relatedness, WordNet assigns different “senses” associated with a particular word to different Synsets. For example, “bank” has ten synsets, such as (a) *Synset('bank.n.01')*: sloping land (especially the slope beside a body of water) and (b) *Synset('depository_financial_institution.n.01')*: a financial

institution that accepts deposits and channels the money into lending activities.

We manually identified the sense of each predicted target word in each sentence context within each triplet. Then, based on the identified senses, we calculated pairwise semantic similarity values using a path-based approach described by Wu & Palmer (ranging from 0 to 1, indicating low to high semantic similarity) (Wu & Palmer, 1994). To check that there were statistically significant differences in the semantic similarity between the predicted words in the *semantically related* and the *unrelated* sentence pairs, we used a permutation approach. Specifically, we computed the mean similarity values for the *semantically related* and *unrelated* pairs separately and took their difference value as our test statistic. We then randomly re-assigned the similarity values across these two types of sentence pairs, re-calculated the mean difference of the permuted values, and took the mean difference value for each randomization (1,000 times) to build a null distribution. We considered the observed test statistic significant if it fell within the highest or lowest 2.5% of the null distribution. This analysis confirmed that the predicted words in the *semantically related* pairs were indeed more semantically similar (mean WordNet semantic similarity = 0.58, SD = 0.29) than the predicted words in the *unrelated* pairs (mean WordNet semantic similarity = 0.25, SD = 0.16, $p < 0.001$).

We used the same methods to determine whether the semantic similarity of the predicted words differed between the *form-related* and *unrelated* sentence pairs. We found a small but significant difference (*form-related* vs. *unrelated*: mean = 0.30 vs. 0.25, SD = 0.18 vs. 0.16, $p = 0.011$). As discussed in the *Results*, to ensure that this difference did not confound the form neural similarity effect, we carried out an RSA using a subset of *unrelated* pairs (56 in total) in which the semantic similarity of the predicted target words as well as other properties of the pre-target words were matched with the *form-related* pairs.

Semantic similarity between pairs of pre-target words

We also examined the semantic similarity between the pre-target words within each pair. Because these pre-target words varied in their syntactic category, instead of using WordNet, which only provides semantic similarity values for words within the same syntactic category (Loper & Bird, 2002), we used Word2Vec (Mikolov et al., 2013). We computed the cosine distance between the 300-dimensional vectors that corresponded to each pair of pre-target words using the Gensim natural language processing library in Python. A permutation-based test showed that the pre-target words in the *semantically related* pairs were slightly more semantically similar than those in the *unrelated* pairs (*semantically related* vs. *unrelated*: Mean Word2Vec semantic similarity

= 0.16 vs. 0.11, SD = 0.26 vs. 0.17, $p = 0.006$). As discussed in the *Results*, to ensure that this difference did not confound our neural similarity effect, we compared the neural similarity values produced by the *semantically related* and a subset of *unrelated* pairs (again in a total of 56 pairs) in which the semantic similarity of the pre-target words as well as other properties of the pre-target words were matched.

We found no significant differences in the semantic similarity of the pre-target words between the *form-related* and *unrelated* pairs (mean = 0.13 vs. 0.11, SD = 0.22 vs. 0.17), $p = 0.17$.

Similarity structure of other properties of the pre-target word

To ensure that any observed neural similarity effects were not driven by other differences in the similarity structure of the pre-target words, we also examined several of their other properties: (1) their lexical probabilities, based on their preceding contexts, which we operationalized using the large language model, GPT-3 (Brown et al., 2020)²; (2) length, i.e., number of letters; (3) orthographic Levenshtein distance (OLD20, Balota et al., 2007); (4) concreteness (Brysbaert et al., 2014); (5) log frequency, based on the SUBTLEX database (Brysbaert & New, 2009); and (6) syntactic class, i.e., whether it was a content or a function word. For each of these variables, we calculated the pairwise absolute difference values and compared these difference values between the *semantically related* and *unrelated* pairs, as well as between the *form-related* and *-unrelated* pairs. Our permutation tests revealed no statistically significant differences (all $ps > 0.09$).

Similarity structure of more general properties of the prior sentence contexts

Finally, we extracted two additional measures for all sentences: (1) context length, i.e., the number of words prior to the target word (this ranged from 4 to 21 words); (2) contextual constraint, i.e., the probability of the most expected target word, as estimated using our cloze norms (this ranged from 67% to 100%). For each of these measures, we calculated the absolute difference values for every pair of contexts. Permutation-based statistical tests once again showed no difference between either the *semantically related* and

unrelated pairs, or between the *form-related* and *unrelated* pairs (all $ps > 0.07$).

Participants

A power analysis showed that a sample size of 34 is required to achieve 80% power for detecting a medium-sized similarity effect ($d = 0.5$: (Wang et al., 2018a, b, 2020); $\alpha = 0.05$ for two-tailed paired t-tests). In total, 36 participants took part in the EEG experiment. The data of three participants were subsequently excluded due to termination of the experiment by one participant and excessive artifacts in two participants, leaving a final dataset of 33 participants (mean age: 20 years, range: 20–28 years; 20 males). All participants were native speakers of English and had no exposure to other languages before the age of 5 years. They were all right-handed with normal or corrected-to-normal vision. They were not taking psychoactive medication, and had never been diagnosed with a psychiatric or neurological disorder. Each participant gave informed consent following procedures approved by the Tufts University Social, Behavioral, and Educational Research Institutional Review Board.

Procedure

The sentences were presented on a computer monitor, positioned approximately 1 m away from the participant, using PsychoPy 2.0 software. Stimuli were presented in white Arial font on a black background, with three characters covering approximately 1° of visual angle. The trial started with a fixation (“++++”) for 1,200 ms, followed by a 400-ms blank. Then, each sentence was presented word by word, with each word being presented for 300 ms, followed by a 400-ms blank screen. The final word was presented together with a period, followed by a 1,200-ms blank. After one-sixth of the trials, at random, participants read a True/False statement based on the sentence that they had just read and judged whether these statements were correct/incorrect by pressing one of two buttons with their left hand. This helped ensure that they read the sentences for comprehension. In all other trials, the word “NEXT” appeared, and participants pressed another button to proceed to the next trial.

All 252 sentences were presented over nine blocks, with each block containing 28 sentences and lasting about six minutes. The experiment lasted about 1.5 h, including EEG preparation, instructions and a short practice session consisting of five sentences.

EEG data acquisition and preprocessing

The EEG dataset was acquired using a Biosemi ActiveTwo system from 64 active electrodes arranged according to the standard 10–20 system montage. Signals were digitized at

² Previous studies have shown that GPT-derived probability values correlate with human-based cloze estimates (e.g. Szewczyk & Federmeier, 2022). Indeed, in the present study, GPT-derived estimates of the lexical probabilities of the predicted target words correlated strongly with the cloze estimates of lexical probability that we had obtained from human participants ($r = 0.92$, $p < 0.001$).

512 Hz, with a passband of DC – 104 Hz. The EEG dataset was preprocessed using Fieldtrip, an open-source Matlab toolbox (Oostenveld et al., 2011). The raw EEG signals were referenced offline to the average of the left and right mastoid electrodes. Visually identified channels with excessive noise were excluded (removed) from further analysis (on average, five out of the 64 channels across participants).³ A fourth-order Butterworth bandpass filter of 0.1–30 Hz was applied to the data to remove slow drift and high-frequency noise (Luck, 2014).⁴ Next, we segmented the data into epochs, which spanned a time window from -1,500 ms to 1,500 ms, relative to the onset of the target word. Trials that exhibited high variance across channels were excluded from further analysis. We then carried out an Independent Component Analysis (ICA; Bell & Sejnowski, 1997), and identified and removed any components that showed temporal and spatial characteristics of eye movements (on average, one component per participant was removed). After these steps, the data were visually inspected and any remaining artifacts were removed. As noted earlier, we excluded the data of two participants who had a trial rejection rate of over 30%. For the remaining 33 participants, 13% of trials (on average) were rejected, with no significant differences in rejection rates across the three types of contexts within the sentence triplets (i.e., dominating-constraining, subordinate-constraining, non-homograph-constraining: $F_{(2,96)} < 1$).

After artifact rejection, there remained, on average, 56 full triplets of trials across all participants. Because we were interested in brain activity reflecting the *pre-activation* of upcoming target words, we did not apply any baseline correction. Instead, we mean-centered activity within each trial by subtracting the average activity of the full epoch from the activity at each sampling point. This approach effectively eliminated any potential shift caused by slow drift.

Representational similarity analysis (RSA)

We carried out a representational similarity analysis (RSA) on the single-trial EEG data (Fig. 1B), using MATLAB 2020a (MathWorks) together with custom-written scripts. When combining EEG/MEG with RSA, one can potentially examine similarities amongst spatial patterns,

temporal patterns, or a combination of both, depending on the research question. For example, in a previous MEG study (Wang et al., 2018b), we examined spatial and temporal patterns separately because we were interested in detecting item-specific *spatial patterns* at the head surface (stemming from distributed underlying sources), and in source localizing the specific neuroanatomical regions that produced item-specific *temporal patterns*. In another MEG and EEG study (Wang et al., 2020), we only examined spatial patterns because we were interested in detecting the pre-activation of animacy-related semantic features at the head surface (again assumed to stem from distributed underlying cortical sources). In the present EEG study, our primary goal was to determine whether there was *any* evidence for a dissociation in the pre-activation of meaning versus form. Therefore, following previous RSA studies (e.g., Choi et al., 2021; He et al., 2021; Lyu et al., 2019), we *combined* spatial and temporal information to maximize our chances of detecting pre-activation effects.

In each participant, on each trial, we extracted vectors of EEG data that represented the spatiotemporal patterns of activity produced across all EEG channels at consecutive sampling intervals. We chose a sampling interval of 31 ms because this corresponded to a full cycle of oscillatory activity at approximately 30 Hz – the low-pass filter that we applied during pre-processing.⁵ Given the 512-Hz sampling rate, each 31-ms sampling interval contained 16 data points. Thus, each sampling interval captured sufficient temporal information while maintaining reasonable temporal precision. Within our time window of interest, i.e., -700 to 0 ms relative to the onset of the target words, at each successive sampling interval, using a step size of one sampling point, we computed a Pearson's *r* value for every pair of trials and averaged these values across all *semantically-related* pairs (*financial* “bank” – “loan”) and across all *unrelated* pairs. We replaced the values of any sampling interval that lay outside the time window of interest with zeros (see Michelmann et al., 2016).

As discussed in our previous work (Wang & Kuperberg, 2023; Wang et al., 2020), Pearson's *r* neural similarity measure can capture *both* item-specific and non-item-specific activity (i.e., evoked responses). The large number of *unrelated* pairs across triplets (31,374 pairs) provided a highly reliable measure of non-item-specific neural similarity (Wang et al., 2018b). Therefore, to isolate the effect of item-specific semantic similarity, at each sampling point from the onset of the pre-target word ($t = -700$ ms) until target word onset ($t = 0$), we carried out paired t-tests comparing

³ We chose to exclude rather than interpolate bad channels to avoid any potential distortion of spatiotemporal patterns over the entire set of channels, which would occur if the true electrical activity at a bad channel was not highly correlated with activity at its neighboring channels.

⁴ High-pass filters can sometimes produce spurious multivariate effects (van Driel et al., 2021) and/or distort the timing of such effects (Acunzo et al., 2012). However, when we carried out the RSA without applying any high-pass filter, we found qualitatively similar effects.

⁵ Following a reviewer's suggestion, we repeated the RSA using different sampling interval sizes (i.e., 0 ms, 20 ms, and 40 ms). We found qualitatively similar effects for all interval sizes.

the neural similarity values produced by the *semantically related* and the *unrelated* pairs. We took the same approach to isolate the effect of item-specific form similarity.

To account for multiple comparisons, we used cluster-based permutation tests (Maris & Oostenveld, 2007). Adjacent data points that showed effects at $p \leq 0.05$ were considered temporal clusters, and within each cluster, we summed the individual t-statistics and took the summed t-value as the cluster-level test statistic. We then built a permutation distribution by randomly shuffling the conditional labels of the neural similarity values at all time points in all participants 10,000 times. We calculated cluster-level statistics on each permutation and selected the largest cluster-level statistic to construct a null distribution. We compared the observed cluster-level test statistic against this null distribution, and took any temporal clusters falling within the highest or lowest 2.5% of the distribution to be significant.

To visualize the item-specific semantic and form pre-activation effects, we subtracted the average neural similarity values produced by *unrelated* pairs from those produced by the *semantically related* pairs and *form-related* pairs. The time series of neural similarity values produced by all three types of sentence pairs are shown in the Online Supplementary Materials (OSM).

Finally, we compared the *timing* of the *form* and *semantic* pre-activation effects. For this analysis, we took a bootstrapping approach because of its flexibility and robustness, even when the distribution of the underlying data is unknown (e.g., Manly, 1997). First, we identified the peak latency for each effect, based on its smoothed grand-average time course (for smoothing, we used a moving average of 20 sampling points). We then calculated the difference between the two identified peak latencies and compared this value against a sampling distribution, which we built by resampling the neural similarity effect of all participants with replacement 5,000 times, and taking the difference in the identified peak latencies between -700 and 0 ms for each iteration. We considered the observed peak latency difference to be significant if it fell within the highest or lowest 2.5% of the sampling distribution.

Results

Semantic pre-activation effect

When we compared the neural similarity values produced by pairs that predicted semantically-related words with those produced by pairs that predicted unrelated words, we found a significant effect between -391 and -309 ms before the onset of the predicted target word, i.e., between 309 and 391

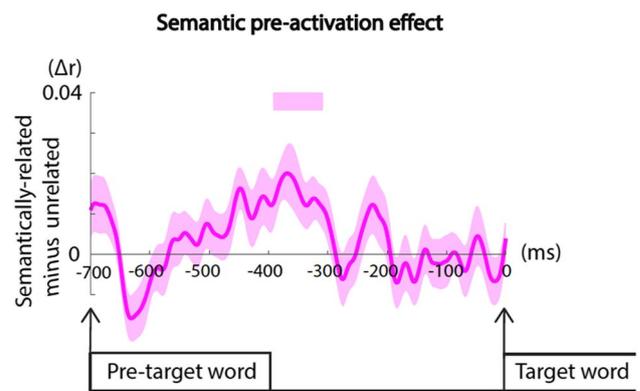


Fig. 2 The time course of the semantic pre-activation effect. Shown is the mean difference in neural similarity values between the *semantically related* and *unrelated* pairs (Δr). Standard errors are indicated with shading. Between -391 and -309 ms before the onset of the predicted target word, i.e., between 309 and 391 ms after the onset of the pre-target word, indicated with the pink horizontal bar, the *semantically related* pairs produced significantly greater neural similarity values than the *unrelated* pairs. The predicted target word was presented at 0ms, and the pre-target word was presented at -700 ms, with a duration of 300 ms

ms following the onset of the pre-target word (cluster-based permutation test: $p = 0.003$); see Fig. 2.

As noted in the Methods, pairs of *pre-target* words were also slightly more semantically similar in the *semantically related* sentence pairs than in the *unrelated* sentence pairs. Therefore, to ensure that the observed effect was driven by the semantic similarity between the *predicted* upcoming words, rather than the pre-target words, we selected a subset of *unrelated* pairs in which the pre-target words were matched on semantic similarity as well as other properties of the pre-target words with the *semantically related* pairs. This analysis again revealed a significant effect (between -412 and -320 ms prior to the onset of the target word, i.e., between 288 and 380 ms following the onset of the pre-target word, $p = 0.001$). This suggests that the neural similarity effect indexed the pre-activation of semantic features of the upcoming target word rather than the semantic features of the pre-target word.

Finally, to ensure that the observed effect was not driven by the general differences in the semantic similarity of the prior context, we carried out a cluster-based permutation test from -1,400 to -700 ms *before* the onset of the pre-target word. We found no significant difference between the *semantically related* and *unrelated* pairs ($p = 0.169$).

Form pre-activation effect

When we compared the neural similarity values produced by pairs that predicted form-related words with those produced by pairs that predicted unrelated words, we found a

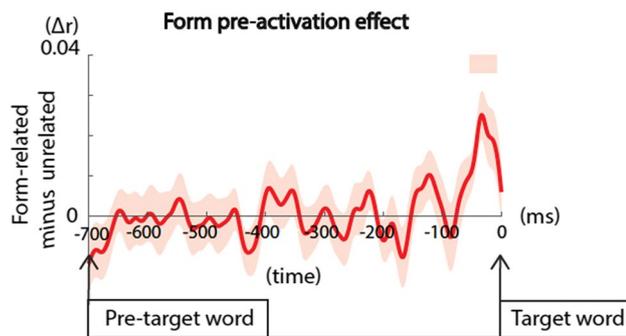


Fig. 3 The time course of the form pre-activation effect. Shown is the mean difference in neural similarity values between the *form-related* and *unrelated* pairs (Δr). Standard errors are indicated with shading. Between -53 ms and -8 ms before the onset of the predicted target word, i.e., between 647 and 692 ms after the onset of the pre-target word (indicated with the red horizontal bar), the *form-related* pairs produced significantly greater neural similarity values than the *unrelated* pairs. The predicted target word was presented at 0 ms, and the pre-target word was presented at -700 ms, with a duration of 300 ms

significant effect between -53 ms and -8 ms before the onset of the target word, i.e., between 647 and 692 ms following the onset of the pre-target word (cluster-based permutation test: $p = 0.025$); see Fig. 3.

As noted in the *Methods*, pairs of the predicted target words were very slightly more semantically similar to each other in the *form-related* sentence pairs than in the *unrelated* sentence pairs. However, when we repeated the analysis using a subset of *unrelated* pairs in which the predicted target words were matched in semantic similarity with the *form-related* pairs, we again found a significant effect (between -47 and -8 ms prior to the onset of the target word, i.e., between 653 and 692 ms following the onset of the pre-target word), $p = 0.025$.

Timing of the semantic pre-activation effect versus the form pre-activation effect

The analysis above suggested that the semantic pre-activation effect preceded the form pre-activation effect, with the semantic pre-activation effect peaking at -367 ms, and the form pre-activation effect peaking at -25 ms, each relative to the target word onset. To determine whether this difference in peak latency was statistically significant, we used a bootstrapping sampling approach. This confirmed that the peak latency was significantly earlier for the semantic pre-activation than the form pre-activation effect ($t_{(32)} = 7.29$, $p < 0.001$).⁶

⁶ Following a reviewer's request, we carried out two additional post hoc tests. First, we statistically compared the peak latency difference between the semantic and form similarity effects using a Jackknife resampling approach. This also showed a significant effect. Second, we directly compared the neural similarity values produced by the

Discussion

A fundamental question in language comprehension is whether the brain generates predictions of both the meaning and the form of upcoming words during language comprehension. In the present study, we addressed this question by combining EEG with RSA. We found that, relative to *unrelated* pairs, pairs of contexts that predicted words with related meanings but distinct linguistic forms (e.g., *financial* “bank” – “loan”) produced more similar neural patterns from 300 to 400 ms before the onset of the predicted target. Conversely, pairs of contexts that predicted words with the same form but different meanings (i.e., homographs, e.g., *financial* “bank” – *river* “bank”) produced more similar neural patterns immediately before target word onset.

Although contexts that predict *semantically related* words are naturally more similar to one another than those that predict *unrelated* words, we detected a semantic pre-activation effect even when the semantic similarity of the pre-target words was matched between the *related* and *unrelated* pairs, and the effect only became significant *after* pre-target onset. We also ensured that the similarity of both types of *related* pairs was matched to that of the *unrelated* pairs with respect to context length and contextual constraint, as well as multiple other properties of the pre-target words (word length, orthographic neighborhood, concreteness, word frequency, syntactic category, and lexical predictability). We therefore take these neural similarity effects as evidence that the meaning and form of the expected words were predictively pre-activated before new bottom-up input became available.

Pre-activation of meaning

Our finding of a semantic pre-activation effect provides direct support for the theory that comprehenders use prior contexts to pre-activate the semantic features associated with expected upcoming words. Previous support for this theory has been somewhat indirect, coming from studies reporting facilitated processing of unexpected words that share semantic features with expected words (e.g., Federmeier & Kutas, 1999). In the present study, our use of RSA allowed us to directly capture neural

Footnote 6 (continued)

semantically related and *form-related* pairs within the two time windows that revealed significant differences in the analysis above, i.e., in comparison with the *unrelated* control condition. Between -391 and -309 ms, the *semantically related* pairs produced greater neural similarity values than the *form-related* pairs although this effect was marginal ($t_{(32)} = 1.99$, $p = 0.055$). Between -53 and -8 ms, the *form-related* pairs produced significantly greater neural similarity values than the *semantically related* pairs ($t_{(32)} = 2.53$, $p = 0.017$).

representations of these pre-activated semantic features before the arrival of new bottom-up input. For example, the semantic features associated with the pre-activated word “bank” and “loan” (e.g., <financial>, <service>) overlapped with each other. In the brain, semantic features are thought to be represented in a distributed fashion across multiple cortical regions (Huth et al., 2016), which project to the scalp surface as unique spatiotemporal patterns. Therefore, the spatiotemporal patterns produced by predicted words that shared semantic features were more similar than those produced by predicted words in *unrelated* pairs that shared no semantic features. This finding also extends our previous RSA work showing that comprehenders also pre-activate distributed semantic features in contexts that, instead of constraining for single words, constrain for broader semantic categories such as animacy (e.g., <animate> following “*The lifeguard cautioned the ...*”) (Wang et al., 2020).

Pre-activation of word-form

Of even greater theoretical significance is our finding of an increase in similarity between the neural patterns produced by predicted words that overlapped only in their linguistic form. As outlined in the Introduction, several studies have claimed to find evidence of form-level prediction. Again, however, this previous evidence primarily comes from ERP studies that examined the *effects* of prior predictions on processing new bottom-up input. Moreover, the interpretation of these ERP effects is challenging, particularly as some findings have not been replicated (Nieuwland, 2019; Nieuwland et al., 2018).

In the present study, our use of RSA methods, in combination with our novel homograph design, allowed us to circumvent many of these interpretational issues, and to directly dissociate the pre-activation of linguistic form from meaning. For example, in the contexts, “*I went to deposit the check at the ...[bank]*” and “*The muddy sides of the river are called the river ...[bank]*”, the predicted concepts (<financial-bank> and <river-bank>) do not share common semantic features. However, both concepts are associated with the same word-form, “BANK”. In the brain, form features are thought to be encoded in a distributed fashion along the posterior ventral visual pathway (Dehaene et al., 2005). Therefore, when projected to the scalp surface, the pre-activation of these same word-forms produced spatiotemporal patterns that were more similar to one another than the patterns produced by predicted words in the *unrelated* pairs that did not share word-form features. As such, our findings provide direct neural evidence that, at least in highly constraining sentences, the brain is able to generate predictions not only at the level of semantic features, but also

at level of specific word-forms (see Kuperberg & Jaeger, 2016, Section 5).⁷

The pre-activation of meaning preceded the pre-activation of form

Our findings also shed important light on *when* the meaning and form of pre-activated words became available. The pre-activation of semantic features was detected ~300 ms after the onset of the pre-target word. This is consistent with previous RSA studies (Hubbard & Federmeier, 2021; Wang et al., 2018b, 2020), suggesting that the brain uses prior contexts to generate semantic predictions as soon as it is able to do so. Also consistent with our previous RSA studies using different presentation rates (1,000 ms per word: Wang et al., 2018b; 550ms per word: Wang et al., 2020), the effect was transient – lasting for only 100 ms and disappearing 400 ms before the onset of the target word.

In contrast, the form pre-activation effect was detected later – ~600 ms following the onset of the pre-target word, i.e., ~100 ms prior to the target word. This later detection of word-form pre-activation is consistent with hierarchical predictive accounts of language comprehension, including predictive coding, which posit that pre-activated information is propagated down the linguistic hierarchy over time – from higher-levels representing semantic features to lower levels that represent form features (e.g., see Kuperberg & Jaeger, 2016, Section 5).

Notably, the time lag between the semantic and word-form pre-activation effects was relatively long – 300 ms. This mirrors the temporal separation between conceptual

⁷ A reviewer raised the possibility that the form pre-activation effect actually reflected an indirect semantic pre-activation effect. On this account, the pre-activation of a homograph’s contextually appropriate meaning (e.g., <financial-bank>) *indirectly* led to the additional pre-activation of its contextually inappropriate meaning (e.g., <river-bank>), and so the form pre-activation effect that we detected actually reflected overlap of these indirectly pre-activated semantic features. Note that this account would still be consistent with the claim that comprehenders pre-activate upcoming word-form forms. This is because the only way that the alternative meaning of the homograph could have been pre-activated is if its *form* was also pre-activated. Nonetheless, we explored this possibility by carrying out a post hoc analysis that contrasted the neural similarity values produced by *indirectly related* pairs (e.g., *river* “bank” – “loan”) with those produced by the *unrelated* pairs, each averaged across the -53 to -8 ms time window time window where we detected the form pre-activation effect. This analysis did not reveal a significant effect. Of course, this does not exclude the possibility that the alternative meaning of the predicted homographs was pre-activated in another time window. However, a comprehensive investigation of how different meanings associated with homographs are pre-activated goes beyond the scope of the present study. To investigate this, one would need to construct an additional set of highly constraining sentence contexts that predict words that are semantically related to the subordinate meanings of the predicted homographs.

retrieval and word-form encoding during language production (Indefrey & Levelt, 2004). As such, these latency results are consistent with the proposal that strong top-down predictions generated during language comprehension may be implemented by the same circuitry that supports language production (Federmeier, 2007; Martin et al., 2018; Pickering & Garrod, 2013).

On the other hand, it is important to consider an alternative account of why the form pre-activation effect was detected so late: It is possible that participants actually pre-activated word-form information earlier, but that this pre-activation was difficult to detect using our signal-averaging methods. Word-form features are thought to be encoded over a shorter time scale than semantic features (Kiebel et al., 2008). Therefore, any jitter in the timing of a highly-transient word-form pre-activation effect across trials would have made it difficult to detect the initial generation of form-level predictions. However, immediately before the presentation of the upcoming word, when this pre-activated information became relevant for bottom-up form-level analysis, its latent representation might have been “reignited,” and brought into an active state across all trials (Sprague et al., 2016; Stokes, 2015), making the word-form pre-activation effect easier to detect.

To investigate this possibility, future studies could carry out the same experiment using a faster presentation rate (e.g., 500 ms per word). If the form-level pre-activation effect disappears at this faster rate, then this would imply that there was not enough time for pre-activation to reach form features before the arrival of new bottom-up input, and that the interval between the pre-activation of meaning and form is fixed (i.e., 300 ms). This would provide support for a prediction-by-production account in which the generation of form-level predictions is limited to slow presentation rates (see Ito et al., 2016). If, on the other hand, a form pre-activation effect can still be detected just before the presentation of the target word, then this would suggest that such predictions are generated earlier and brought online just before they are needed, regardless of presentation rate. This would, in turn, imply that, in predictive contexts, form-level predictions are generated rapidly and routinely during real-time natural language comprehension (DeLong et al., 2021).

Conclusion

To summarize, by combining EEG with RSA, we provide direct neural evidence for the pre-activation of both the meaning and form of expected words in predictive language contexts. Moreover, our finding that the pre-activation of meaning preceded the pre-activation of form is consistent with hierarchical predictive accounts of language comprehension, which posit that information flows from higher to

lower levels of linguistic representations before new input becomes available.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.3758/s13423-023-02385-0>.

Acknowledgements This research was supported by the National Institutes of Health under Award Number R01HD082527. We thank Sophie Greene, Feng Cheng, and Edward Alexander for their assistance with stimuli preparation and data collection.

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Open Practices Statement The data and materials for the experiment are available at <https://osf.io/u6tpx/>. The experiment was not preregistered.

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