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Neural correlates of semantic prediction and resolution in sentence processing

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Abstract

Most brain imaging studies of language comprehension focus on activity following upon meaningful stimuli. Testing adult human participants with high-density EEG, we show that, already before the presentation of a critical word, context-induced semantic *predictions* are reflected by a neurophysiological index, which we therefore call the Semantic Readiness Potential (SRP). The SRP precedes critical words if previous sentence context constrains the upcoming semantic content (High-constraint contexts), but not in unpredictable (Low-constraint) contexts. Specific semantic predictions were indexed by SRP sources within the motor system – in dorsolateral hand motor areas for expected *hand-related* words (e.g. “write”), but in ventral motor cortex for *face-related* words (“talk”). Compared to affirmative sentences, negated ones led to medial prefrontal and more widespread motor source activation, the latter being consistent with predictive semantic computation of alternatives to the negated expected concept. Predictive processing of semantic alternatives in negated sentences is further supported by N400 responses, which showed the typical enhancement to semantically-incongruent sentence endings only in High-constraint affirmative contexts, but not to High-constraint negated ones. These brain dynamics reveal the interplay between semantic prediction and resolution (match vs. error) processing in sentence understanding.

Significance Statement

Most neuroscientists agree on the eminent importance of predictive mechanisms for understanding basic as well as higher brain functions. This contrasts with a sparseness of brain measures that directly reflect specific aspects of prediction, as they are relevant in the processing of language and thought. Here, we show that, when critical words are embedded in predictive sentence contexts, a predictive brain response reflects specific meaning features of anticipated symbols already before they appear. The granularity of the semantic predictions was so fine-grained that the cortical sources in sensorimotor and medial prefrontal cortex even distinguished between predicted *face-* or *hand-related* action words (for example the words "lick" or "pick") and between affirmative and negated sentence meanings.

Introduction

Current theories of brain function emphasize the importance of predictions for perception, action and language processing (Egner et al., 2010; Friston and Frith, 2015). In language understanding, we frequently know what speakers intend to say before they complete their utterances (Sacks et al., 1974) and even single words can be identified before their ends (Marslen-Wilson, 1987). Still, most experimental studies on language focused on processes following, not preceding, the critical expected words (Schwanenflugel and Shoben, 1985; Van Petten and Luka, 2012). The well-known N400 event-related brain potential (ERP) (Kutas and Federmeier, 2011) reflects the degree to which critical words are semantically expected in a given context, thus possibly indexing the word-circuits' level of context-induced pre-activation (DeLong et al., 2005; Otten et al., 2007; Ito et al., 2016). Although the N400 is informative about predictive language comprehension, it *follows* the (un)expected words and, therefore, the point in time when predictions first arise. If *semantic* predictions determine the way we process language, a direct neurophysiological index of meaning expectancy, *preceding* the critical linguistic items, will be of crucial importance. Recent studies reported neurophysiological correlates of predictions, which preceded the expected language units in the processing of single words (Pulvermüller et al., 2006; Dikker and Pylkkanen, 2013; Söderström et al., 2016), noun phrases (Fruchter et al., 2015), and sentences (Maess et al., 2016), although brain indexes of fine-grained semantic aspects of an expected utterance are still missing. A degree of semantic specificity is suggested by an anticipatory frontocentral potential, which emerges when subjects expect visual (Kilner et al., 2004) and acoustic (Grisoni et al., 2016) stimuli signifying body actions. This anticipatory activity resembles the readiness potential (RP), a brain indicator of intentions to move (Kornhuber and Deecke, 1965). Using high-density electroencephalography (128-channel EEG), we here report a *semantic readiness potential*, SRP, which emerges during sentence processing and reflects aspects of the meaning of predictable action words before they appear.

To obtain contexts inducing specific action-semantic expectations, we created affirmative High-constraint (AHC) sentence fragments, upon which specific *face-* or *hand-related* action words were reported to follow with high probability. Control conditions displayed the same sentences with negation, thereby cancelling the expectation of specific words (negated Low-constraint, NLC sentences). To separate brain indexes of predictability from those of negation (Tettamanti et al., 2008), we also investigated negated High-constraint (NHC) sentences including predictable action words (**Table 1**).

HC contexts inducing expectations of specific words may specifically pre-activate the neuronal circuits processing these words. Therefore, an SRP was expected in HC contexts but not in LC sentences. Crucially, if semantic aspects of predictable words are reflected before critical word onset, the SRP should differ between contexts predicting words with different meanings. We took advantage of previous works in which action words (e.g., "*bite*" vs. "*grasp*") activated their related body-part-representation in sensorimotor cortex (i.e. "*mouth*" vs. "*hand*") (Hauk et al., 2004). Therefore, the SRP in AHC contexts may reflect specific semantic predictions by differentially activating sensorimotor cortex. In case negation is reflected in specific brain processes (Fischler et al., 1983; Nieuwland and Kuperberg, 2008), its effects may include the anticipation of multiple semantic alternatives (NHC condition); note that negation implies that the predictable proposition is not true, therefore giving rise to considering alternative action possibilities (Kühn and Brass, 2010), which may be manifest in broader sensorimotor activation.

The predictive semantic processes have further implications for the brain responses following the critical word (Holcomb and Neville, 1990). As no specific semantic prediction is possible in NLC sentences, all target words were semantically unexpected so that generally large N400s were hypothesized. In contrast, the AHC condition led to specific action-semantic expectations, which were violated by incongruent endings, so that only these should lead to large N400s. Because negated predictive contexts imply the processing of both target words and semantic alternatives, a further prediction was the reduction of the N400 to critical words in NHC contexts independent of sentence congruency (**Table 1**).

Table 1 about here

Materials and Methods

Participants. Twenty-five healthy adults (mean age 24.1 years, range: 20-29; 14 females) participated after giving informed written consent. All participants were monolingual English native speakers, who had not learned any second language before the age of 8 years. All participants had normal hearing, normal motor control, normal or corrected-to-normal vision and no record of neurological or psychiatric disease. One participant was excluded due to excessively noisy EEG signals. Therefore, data from twenty-four participants (mean age 24.1 years, range: 20-29; 14 females), all of them strongly right-handed as determined by the Oldfield handedness inventory (Oldfield, 1971) (mean laterality quotient 80.6 ± 14.9 s.d.), were used for the EEG analysis. Participants provided written informed consent prior to participating in the study; procedures were approved by the Ethics Committee of the Charité Universitätsmedizin, Campus Benjamin Franklin, Berlin, Germany.

Stimuli and experimental design. 138 'congruent' English sentences were constructed and grouped into six categories of 23 sentences each on the basis of both the target verb they contained (i.e. *face-* or *hand-related*) and the sentence type and context in which the word was embedded (i.e. Affirmative High-constraint [AHC], Negative High-constraint [NHC], and Negative Low-constraint [NLC]).

First, triplets of semantically similar sentences were created whose final words were either *face-* or *hand-related* action words. Each triplet included one of the sentence types: AHC - "*I VERB PHRASE and I VERB …"* (e.g. *"I take the pen and I write"*) - NHC - "*I VERB PHRASE but I do not VERB*" (e.g. *"I take the pen but I do not write"*) - and NLC: "*I do not VERB PHRASE and I VERB*" (e.g. *"I do not take the pen and I write"*) (**Table 1**). The target words were selected on the basis of an evaluation carried out by 10 English native speaker participants (mean age 28.3 years, ± 5.19 s.d.; 6 female), who did not take part in the EEG experiment. They were asked to complete fragments of each sentence missing the sentence final verb, and list words they would expect in these contexts (cloze test). Participants had to read sentence fragments one-by-one and write up to three possible completions. The fragment order was randomized across participants. Data showed similar and hypothesis-based modulation of expected semantic types with the repeated-measures ANOVA revealing a main effect of the 3-level factor Context ($F_{2,44} = 671.203$, $p < 0.001$, $\eta p^2 = 0.97$) (Figure 1b). Bonferroni corrected planned comparison tests revealed that the NLC sentences were completed with more uncertainty as compared with AHC ($p < 0.001$) and NHC ($p < 0.001$), with no significant difference between the latter two ($p = 1$).

Target words were semantically-related to the sentence fragments (e.g., pen - write), they had a predominant use as verbs and included one or two syllables; the two semantic word categories, *face-* and *hand-related* action words, were matched for mean word length (average of letters: *face-related*: 4.1 ± 0.81 s.d.; *hand-related*: 4.6 ± 0.89 s.d.) and standardized word frequency, computed as the logarithm of the number of occurrences of a word form within the British National Corpus (http://corpus.byu.edu/bnc/) (average: *face-related* = 3.37 ± 0.51 s.d.; *hand-related* = 3.44 ± 0.67 s.d.; t = 0.37, p = 0.72).

Furthermore, the following features were implemented to exclude possible confounds: Sentence contexts further constrained target words to be understood as verbs, as words of different grammatical category may elicit different ERPs (Nobre and McCarthy, 1995). All sentences were in first person singular present active form, as conjugation of action words may modulate cortical activity (Papeo et al., 2011). Sentences could be used as statements or reports; untypical words and non-literal usage were avoided (i.e. technical terms, long compounds, proverbs and idioms). Sentence length was matched between *face-* and *hand-related* sentences (average of words within the AHC context: *face-related*: 8.8 ± 1.7 s.d.; *hand-related*: 8.1 ± 1.3 s.d). Because it is difficult to find sufficient numbers of words with specific semantic features which are also matched for a range of psycholinguistic properties, it was necessary to repeat 3 words of each semantic type (i.e. *face-* and *hand-related* action words). Although word repetition may reduce the word-elicited brain response following the items (Sekiguchi et al., 2001), any such repetition-related ERP-attenuation would affect both semantic word types to the same degree. Furthermore, no data are presently available which address repetition effects on the semantically-predictive brain response appearing before critical word onset, which we first report here. If present, any repetition-related attenuation of anticipatory brain activity would work against finding neurophysiological correlates of semantic differences.

In addition to the sentences ending on target words (‘congruent sentences’), we created 138 semantically incongruent sentences by exchanging the *face*- and *hand-related* critical words between contexts. Specifically, each *face-related* word was replaced in its context with a *hand-related* word similar in length, and vice versa. Therefore, the entire stimulus set consisted of 276 sentences.

We recorded multiple repetitions of all sentences uttered by a female native speaker of English and selected items that were acoustically similar (criteria: length, loudness, intonation contour). The recordings of the critical words from the two semantic categories were matched for fundamental frequency (F0) and sound energy. Finally, the three types of sentence fragments were normalized to the same average sound energy calculated as root-mean-square (RMS) power. The word recognition point (WRP) (Marslen-Wilson, 1987) of the target words was estimated by a single native speaker of English, who was presented with gates of all critical words increasing in length in steps of 50ms (Grosjean, 1980; Pulvermuller et al., 2003). The estimated WRP of a given word was assumed to lie at the gate length of first correct and confident recognition (see Marslen-Wilson, 1987). The average word recognition point was computed as the average of all the *face*- and *hand-related* words. The WRP lay around 450 ms after word onset and did not differ between semantic types (average: *face-related words* = 443 ms, s.d. 142; *hand-related words* = 466 ms, s.d. 93).

The EEG experiment consisted of one experimental block in which the 276 sentences were presented in random order to the participants. We created three separate lists, in each of which the sentences order was randomized; each EEG participant was randomly assigned to one of these lists. The inter-stimulus-interval (ISI) between the end of the sentence fragment constituting the context and the final (target or incongruent) word onset was 1500 ms. This pause was necessary to separate the neurophysiological response following the end of the sentence fragment from any predictive RP-like activity preceding the subsequent action verb. Note however, that this pause did not lead to unnaturally sounding sentences; hesitation phenomena and pauses naturally occur in spontaneous conversation. The inter-trial-interval (ITI) between sentences was 3100 ms. The entire EEG recording lasted approximately 25 minutes.

Apparatus and procedure. The experiment was conducted in the electrically and acoustically shielded chamber of the Brain Language Laboratory, Freie Universität Berlin. Outside the chamber, one personal computer (PC) controlled stimulus presentation, timing and randomization using E-Prime 2.0.8.90 (Psychology Software Tools Inc., Pittsburg, PA, RRID: SCR_009567). Inside the chamber, a separate PC was used to show a silent movie free of human-action (*"The Blue Planet"*, BBC/Discovery Channel Co-Production) to the participants, who were seated 1 meter from the monitor. During EEG recording all the acoustic stimuli were presented binaurally through high-quality headphones (Ultrasone PRO 450, S-LOGIC™). Participants were instructed to focus their attention on the movie and they were told that the acoustic stimuli appearing during the film were of no relevance and should be ignored. After the EEG recording all the participants, seated in front of a PC, were asked to evaluate the entire stimulus set with a cloze-probability test managed with E-Prime 2.0.8.90 software. Participants were instructed as follows: "You will hear several incomplete sentences. Please write down which words you would use to complete each sentence you hear. You can write one, two or three possible completions with one or two words. If you do not have any idea, please don't write anything down". Therefore, the participants had to listen to sentence fragments (i.e. the stimuli sentences without the target word) and write down the words they would expect in the respective contexts. Upon responding, they were presented with the next incomplete sentence. The sentence order was randomized among participants. After completion of this sentence evaluation, subjects were presented one-by-one with the target words from the study and the following semantic ratings had to be made: (i) "How strongly are the following words related to face actions?"; (ii) "How strongly are the following words related to hand/arm actions?" Participants had to listen to the stimuli and click, with the left button of the mouse, on a continuous visual analogue scale, VAS, ranging from 0 (weak) to 100 (strong). The order of the words was randomized, as it was the order with which the two semantic ratings were administered to participants.

Electrophysiological recordings and Pre-processing. The EEG was recorded through 128 active electrodes embedded in a fabric cap (actiCAP 128Ch Standard-2; Brain Products GmbH) and arranged according to the international 10–5 system. Three electrodes (placed above and below the left eye and to the right outer canthus of the right eye) were used to measure vertical and horizontal electro-oculogram (vEOG, hEOG). All electrodes were referenced to an electrode placed on the tip of the nose. Data were amplified and recorded using the BrainVision Recorder (version: 1.20.0003; Brain Products GmbH, RRID: SCR_009443), with a passband of 0.1-250 Hz, sampled at 1000 Hz and stored on a disk. Impedances of all active electrodes were kept below 10 KΩ. Offline analysis started with data down-sampling to 250 Hz. Afterwards, Independent Component Analysis (ICA) with standard parameters for artifact removal, as implemented in EEGLAB 10 (Swartz Center for Computational Neuroscience, La Jolla, CA; http://www.sccn.ucsd.edu/eeglab, RRID: SCR_007292) has been carried out. A component was considered to be artifactual when its topography showed peak activity only over the horizontal or vertical eye electrodes and when it showed a smoothly decreasing power spectrum (which is typical for eye movement artifacts (Delorme and Makeig, 2004). After calculating the independent components, eye blink components were removed from the EEG data. After ICA, offline analysis was carried out with Brain Products' Analyzer 2.0 (BrainProducts GmbH, RRID: SCR_002356). The electrophysiological signal was filtered using a digital 20 Hz low-pass filter that is typical for slow brain potentials (Luck and Kappenman, 2012). Since the only two previous publications on perceptually-induced RPs reported anticipatory activity starting about 400ms (Kilner et al., 2004) and 250ms (Grisoni et al., 2016) before the expected perception, trials were epoched from 480 ms before word onset to 840 ms after. The first 50 ms of the segmentation were used as baseline. Note that studies with overt motor responses sometimes show much earlier RP onsets (Kornhuber & Deecke, 1965), so that action-related perceptions (of pictures or sounds) produced comparatively short RPs. Consistently, preliminary analysis of our present data indicated the first RP-like deflection at ca. 400ms before critical word onset. Epochs with voltage fluctuation > 100 µV and those contaminated with artifacts due to amplifier clipping, bursts of electromyographic activity, or alpha power were excluded from averaging by a semi-automatic rejection procedure. On average, approximately 10% of the trials were rejected because they violated these artifact criteria.

Data Analysis

Stimulus ratings. The predictabilities of critical words to appear after the sentence fragments was defined as the proportion of participants who correctly named the critical word when being presented with the fragment. A 2 x 3 repeated-measures ANOVA with the factors Word-type (*face*- and *hand-related*) and Context (AHC, NHC, NLC) was carried out on these frequencies. The visual analogue scale scores for the two target word categories (i.e. *face*- and *hand-related* words) were analyzed by means of a 2 x 2 repeatedmeasures ANOVA with the factors: VAS (*face-*, *hand-relatedness*) and Word-type (*face*- and *hand-related* words).

Pre-stimulus anticipatory activity.

For investigating *predictive* brain activity in anticipation of action words, the time window of interest ends at the onset of these critical stimuli. The RP develops gradually within several hundreds of milliseconds, with premotor and primary motor activation appearing in its very last part, within 100 ms or shorter before movement or critical stimulus onset (Erdler et al., 2000; Kilner et al., 2004; Edwards et al., 2010; Grisoni et al., 2016). In a sound perception paradigm (Grisoni et al. 2016), we recently found most pronounced somatotopic RP effects during the last tens of milliseconds before predicted sound onset. Therefore, we extracted the mean ERP amplitudes (μV) for the last 100 ms and for the last 20 ms immediately before critical word onset at central electrodes (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2), where the RP is known to be largest (Deecke et al., 1969). First, we tested whether the negative deflection observed was significant in the three contexts. To this end, the average of the mean ERP amplitudes (μV) obtained for the two word-type expectations (i.e. *face*- and *hand-related* words) in each of the three contexts (i.e. AHC, NHC and NLC) were submitted to separate t-tests against zero. Subsequently, we performed a 3 x 2 repeated measures ANOVA with the factors Context (AHC, NHC and NLC) and Expected Semantic Type (*face*- and *hand-related* words). We also investigated possible neurophysiological changes across the experiment, by directly comparing the first twelve trials with the last twelve trials in each context, by calculating a 2 x 3 repeated measures ANOVA with the factors Trials (first, last) and Context (AHC, NHC and NLC). Note that this comparison is important for addressing the possibility of an influence of experiment-specific processing strategies (Neely, 1977), which may develop during the study. In case significant interactions were found, topographical differences between *face*- and *hand-related* word contexts were investigated using a larger array of fronto-parietal electrodes (F7, F3, Fz F4, F8; T7, C3, Cz, C4, T8; P7, P3, Pz, P4, P8). Because the NLC condition did not show reliable RPs, this evaluation focused on the predictable contexts (i.e. AHC and NHC – which both produced clear RPs) (Luck and Kappenman, 2012). In this case, a 2 x 2 x 3 x 5 repeated-measures ANOVA design included the factors Gradient (anterior-posterior, three levels), Laterality (left-right, five levels) along with Context (AHC and NHC) and Expected Semantic Type (*face*- and *hand-related* words).

fMRI and Source localization. Because our main predictions addressed cortical areas relevant for semantic prediction, it was crucial to estimate and compare the sources of the observed neurophysiological responses. Therefore, ERP topographies showing significantly different activation patterns between Contexts and Expected Semantic Types were further analyzed by calculating distributed cortical sources using standard methods implemented in SPM8 (Litvak et al., 2011), which had previously been used in our lab (Grisoni et al., 2016). As any distributed source localization, this method cannot overcome the non-uniqueness of the inverse problem (von Helmholtz, 1853), but successfully uses established priors for providing plausible source solutions for cognitive experiments. The template structural MRI included in SPM8 was used to create a cortical mesh of 8196 vertices, which was then co-registered with electrode cap space using three electrodes as fiducials: Fpz, TP9 and TP10. The volume conductors were constructed with an EEG (3-shell) boundary element model (BEM). The averaged RP responses were then inverted at the group level, using the multiple sparse prior (MSP) technique, specifically the “Greedy Search” algorithm (Litvak and Friston, 2008). In order to achieve good SNRs in estimating cortical sources in each participant for each Expected Semantic Type, source images from the two contexts (i.e. AHC and NHC) were averaged. The same procedure was used for localizing context effects, thus collapsing *face-* and *hand-related* activation maps across the AHC condition and, again, for the NHC context. Activation maps were then smoothed using a Gaussian kernel of full-width half-maximum (FWHM) of 14mm, resulting in 4 images per participant (i.e. *face-* and *hand-related* expected words; AHC and NHC contexts). To test whether the *face-* and *hand-related* Expected Semantic Types differed between each other within the sensorimotor cortices, we carried out voxelwise paired t-tests in predefined regions of interest (ROIs).

As some of the predictions addressed activity in the motor system, two motor ROIs were defined based on the results of a separate fMRI localizer experiment, performed with different subjects. To this end, a group of thirty-one participants (mean age 23.2 years, ±5.3 s.d.; 16 females; mean laterality quotient 91.7 ± 15.3 s.d.; selected with the same criteria as for the EEG experiment), performed lip and hand movements (Hauk et al., 2004). Participants were scanned in a 3T Siemens Tim Trio system (Siemens, Erlangen). The brain regions were defined in relation to a baseline in which the participants were resting. Participants had to perform repetitive lip movement avoiding contact between the lips and fingers movement with the right index finger avoiding contact between finger and hand. Each movement block was 15 seconds long and repeated 4 times, with 15 seconds of rest between blocks. Block order was random. The “peak activation voxel” (largest t value) in fronto-central cortex was selected per movement. The Lips movement > baseline contrast revealed activity located in a ventral pre-central region (-54, -10, 39; $p < 0.001$, FWE corrected at whole-brain level), whereas the Hand movement > baseline contrast revealed activity located in a dorsolateral pre-central region (-36, -18, 62; $p < 0.001$, FWE corrected).

ROIs for the ERP generator localization were created with Marsbar 0.43 (MARSeille Boîte À Région d’Intérêt SPM toolbox, RRID: SCR_009605) and defined as 14-mm-radius spheres (i.e., matching the FWHM of the smoothing parameter) centered at the above-mentioned coordinates. These ROIs were then combined in a unique mask image used as an *Explicit Mask*. Only voxels included in this mask were considered when comparing the sources of *face-* and *hand-related* expected semantic type conditions. Similarly, differences between AHC and NHC contexts within and outside the sensorimotor cortices were tested by means of two sets of paired t-test. A first comparison was carried out on the whole brain, whereas a second hypothesis-driven analysis tested for specific differences within the sensorimotor system. To this end, we created a mask image which included Brodmann areas 1-4 and 6 (i.e. primary motor, premotor and somatosensory areas, respectively) using the WFU_PickAtlas (Maldjian et al., 2003). Finally, in order to test the RP's temporal development, we performed source estimations, using the same methodology, on the ERP obtained by averaging all the High-constraint conditions together. We extracted the ERP activation maps from two non-overlapping time windows, the interval around the maximum of the 100-ms-window before critical word onset (from 80 to 40 ms) and the terminal 20ms window. Thus, per each participant we obtained two images (i.e. one per each time window) that were submitted to t-tests against zero. For fMRI and all the source analyses (t-tests), P values were thresholded at $P < 0.05$ corrected for multiple comparisons using the family-wise error (FWE) procedure; significant clusters were considered only if they included more than 60 voxels.

Post-stimulus potentials. Two word-related potential components were analyzed, the early N100 and the subsequent N400. Since electrophysiological post-stimulus responses are usually reported with a baseline correction computed across the last 100 ms before word onset (Penolazzi et al., 2007) we adopted the same procedure.

N100. First, we assessed the N100 responses on fronto-central electrodes (F1, Fz, F2, FC1, FCz, FC2), where this early component is known to be largest (Vaughan Jr and Ritter, 1970) and therefore the best SNR can be expected. The N100 response was calculated as the mean amplitude in the 40 ms time window centered at 106 ms from word onset. This latency was obtained as the local maximum (within the interval 0 – 200 ms from word onset) of the grand average obtained by collapsing all the conditions together. Potential effects of word and context were assessed with a 3 x 2 x 2 repeated measures ANOVA with the factors Context (AHC, NHC, NLC), Critical Word Type (*face*- and *hand-related* words) and Congruency (congruent and incongruent with respect to context-induced expectations).

N400. Since critical words were presented acoustically and the word recognition point of these items was estimated to be ca. 450 ms after their onset, we expected a late N400-like response

(500-600 ms from word onset). The mean amplitudes extracted from three anterior-posterior midline electrodes (FCz, CPz, POz), canonical sites for the N400 (Penolazzi et al., 2007), were submitted to a 3 x 2 x 2 x 3 repeated measures ANOVA with the factors Context (AHC, NHC, NLC), Semantic Word Type (*face*- and *hand-related* words), Congruency (congruent and incongruent with respect to the expectations) and Gradient (anterior-posterior; FCz, CPz, POz). Additional analyses performed on broader fronto-parietal electrode selections confirmed the results obtained.

For further investigating any significant interaction effects revealed by the ANOVAs, F-tests were used for planned comparisons. All results reported survived Bonferroni correction. Partial eta-square values (ηp^2) are reported as indexes of effect sizes. When sphericity violations were found in the ANOVAs, Greenhouse-Geisser correction was applied and corrected p-values are reported.

Figure 1 about here

Results

Stimulus ratings. Participant ratings confirmed that affirmative and negated High-constraint sentence contexts were comparable with regard to the probabilities with which their critical congruent words could be determined from sentence context; in contrast, the Low-constraint conditions were confirmed to include unexpected critical words. The repeated measures ANOVA revealed a main effect of the 3-level factor Context ($F_{2,44} = 712.58, p < 0.001, \eta p^2 = 0.97$). Bonferroni corrected planned comparison tests revealed that the NLC sentences were completed with more uncertainty as compared with AHC ($p < 0.001$) and NHC ($p < 0.001$), with no significant difference between the latter two ($p = 1$) (**Figure 1b**). The visual analogue scale (VAS) scores assessing the semantic *face*- and *hand-relatedness* of our words revealed main effects of VAS ($F_{1,23} = 12.68, p = 0.002, \eta p^2 = 0.35$), due to higher scores in the *face*- as compare with the *hand-relatedness* visual analogue scale ratings (p = 0.002), and Word-type ($F_{1,23} = 34.57, p < 0.001, \eta p^2 = 0.60$), due to higher scores for the *face*- as compare with *hand-related* words. Crucially, the cross-over interaction of VAS and Word-type ($F_{1,23} = 295.95, p < 0.001, \eta p^2$

$= 0.93$) was significant, due to higher scores for the *face*- as compare to *hand-related* words in the VAS assessing *face-relatedness* ($p < 0.001$) and, vice versa, higher scores for *hand*- as compare to *face-related* words in the VAS assessing *hand-relatedness* ($p < 0.001$).

Sentence contexts predicting *action-related* words and concepts elicit anticipatory activity reflecting semantic expectation before critical word onset. Both HC conditions elicited a slowly-emerging negative-going potential starting ca. 350 ms before appearance of the critical word stimulus (**Figure 1a,c** and **2a**). The waveforms' smoothly growing shape and their fronto-central scalp distribution (Kornhuber and Deecke, 1965) are consistent with the RP profile. In the last 100 ms before critical word onset, only the High-constraint conditions elicited reliable RPs as documented by t-tests against zero (AHC: mean amplitude = -2.05 µV, $t_{23} = -3.72$, $p = 0.001$; NHC: mean amplitude = -2.04 µV, $t_{23} = -4.42$, $p = 0.0002$; NLC: mean amplitude = 0.02 µV, $t_{23} = 0.05$, $p = 0.96$ *n.s.*). Repeated measures ANOVA performed on this time window revealed a significant main effect of Context ($F_{2,46} = 6.61$, $\varepsilon = 0.95$, *adjusted* $p = 0.003$, $\eta p^2 = 0.22$) with Bonferroni corrected planned comparison tests revealing that the NLC context induced weaker anticipatory activity as compared with AHC ($p = 0.008$) and NHC ($p = 0.009$), with no significant difference between the latter two ($p = 1$). The repeated measures ANOVA comparing the RP amplitudes in the three contexts extracted for the first and the last twelve trials of the experiment confirmed the significant main effect of Context ($F_{2,46} = 4.33$, $\varepsilon = 0.98$, *adjusted* $p = 0.019$, $\eta p^2 = 0.16$) observed on the whole dataset, but gave no evidence of a change of RP signatures across the experiment; this result fails to confirm a physiological manifestation of experiment-induced strategies developing across the study (see **Methods**). Repeated measures ANOVA on a larger array of fronto-parietal electrodes at the end of the RP curves and before word onset revealed a main effect of Laterality ($F_{4,92} = 3.18$, $\varepsilon = 0.59$, *adjusted* $p = 0.042$, $\eta p^2 = 0.12$) with Bonferroni corrected planned comparison revealing a topographical distribution consistent with the RP profile (Shibasaki and Hallett, 2006) in right-handed participants, where the central electrodes show larger amplitudes as compare with most right-hemispheric recording sites ($p = 0.02$) but not relative to the most left-lateral ones ($p = 1$). Furthermore, the anticipatory activity was modulated in its topographical distribution by the semantic type of the expected words (i.e. *face-* or *hand-related*) as revealed by significance of the interactions between the factors Expected Semantic Type, Gradient and Laterality ($F_{8,184} = 3.7$, $\varepsilon = 0.37$, *adjusted* $p = 0.015$, $\eta p^2 = 0.14$). Finally, also the Context affected the ERP topographies as revealed by a Context by Gradient ($F_{2,46} = 4.57$, $\varepsilon = 0.73$, *adjusted* $p = 0.027$, $\eta p^2 = 0.17$) interaction. These results demonstrate that semantic features of the context are manifest in the anticipatory potential, which we therefore call the *semantic readiness potential* or *SRP*.

Figure 2 about here

Distributed sources underlying the SRP were calculated to determine its cortical generators. First we investigated source estimations for SRP collapsed across all predictable conditions. t-tests against zero revealed generators located in areas traditionally associated with semantic processing, including the anterior temporal areas and the inferior prefrontal cortex (Bookheimer, 2002; Patterson et al., 2007) (BA 45/46) (**Figure 1d**). Comparisons between contexts revealed generator clusters specific to the Expected Semantic Type, which were located in the somatosensory and motor areas bilaterally and in dorsolateral prefrontal cortex (BA 9) (**Table 2** and **Figure 1d**). To better disentangle this complex pattern of activations, SRP sources were compared between affirmative and negated contexts (i.e., AHC vs NHC) and between specific semantic expectations (i.e. *face-* vs *hand-related actions*). Just before word appearance, where ERP data had indicated topographical dissociations between Expected Semantic Type and Contexts, the whole brain AHC > NHC contrast revealed a significant cluster located in the left inferior frontal region, whereas the opposite NHC > AHC contrast revealed significant clusters located in temporal pole, temporoparietal junction (TPJ) and dorsolateral prefrontal cortex (BA 8 and 9, **Figure 2c** and **Table 2**). The same contrast restricted to sensorimotor areas (i.e. BA 1-4, 6, see **Methods**) revealed a more widespread motor activation in the NHC as compare to the AHC context (**Figure 2d** and **Table 2**). The reverse contrast did not yield significance.

When testing for semantic specificity of the RP brain generators, whole brain corrected comparisons were not significant. Hypothesis-driven focusing on regions of interest (ROIs) in the motor system, namely on face and hand representations, showed relatively larger activation in the ventrolateral pre-central areas for contexts predicting *face-related* word and the reverse, greater activation for *hand-* as compare with *face-related* item expectation, in dorsolateral pre-central areas (**Figure 2b** and **Table 2**).

N400s elicited by critical words show interactive effects of sentence polarity and prediction matching. As much previous research found neurophysiological effects to critical words violating context-induced semantic predictions in the N400 component (Kiefer and Martens, 2010) (**Figure 3a,d**), ERPs elicited by the critical words were calculated relative to a 100 ms baseline before critical word onset, as is standard practice (Kutas and Federmeier, 2011). **Figure 3** shows that the word-elicited potentials included an early positive deflection (P50), followed by a negative-going peak at approximately 100ms (N100), a positive going wave maximal at approximately 200ms (P200) and a subsequent negative-going deflection (N400). Significant differences were absent for the early components, possibly due to acoustic variance across spoken word onsets. N400 mean amplitudes revealed a main effect of Context ($F_{2,46} = 4.73$, $\varepsilon = 0.88$, *adjusted* $p = 0.017$, $\eta p^2 = 0.17$) with Bonferroni corrected planned comparison tests showing that NLC contexts induced larger N400 responses than NHC ($p = 0.01$) but not relative to AHC conditions ($p = 0.48$), with no significant difference between the latter two ($p = 0.32$). Critically, there was a significant interaction between the factors Context and Congruency ($F_{2,46} = 4.12$, $\varepsilon = 0.84$, *adjusted* $p = 0.029$, $\eta p^2 = 0.15$), with planned comparison tests revealing that the expectancy violation in the AHC context produced a larger N400 response than expected congruent critical words ($p = 0.03$), whereas NHC or NLC contexts did not reveal any N400 modulation by word expectancy (both $p = 1$) (**Figure 3d**). Crucially, whereas NLC contexts elicited large N400s throughout, the N400 response was virtually absent after NHC sentence fragments. Specifically, the NHC incongruent condition elicited a significantly smaller negative-going response in the N400 interval compare with both AHC ($p = 0.006$) and NLC contexts ($p = 0.01$), with no significant difference between the latter two ($p = 1$). These results are evidence for true prediction violations in the incongruent AHC condition and both NLC conditions, but not in any of the NHC contexts. It appears that there is no truly unexpected word in the latter case, possibly because subjects were entertaining alternative hypotheses. These results confirm the prediction based on the hypothesis that multiple alternatives are activated in negated predictable sentence processing.

Figure 3 about here

Discussion

This study shows the emergence of an RP in complex sentence contexts *before semantically predictable words* but not before unpredictable ones. Intriguingly, different semantic readiness potential (SRP) topographies and different cortical source constellations were found in anticipation of words with different meanings, therefore proving specific semantic information in predictive brain activity before the anticipated meaningful symbols appeared. Predicted words related to actions typically performed with different effectors (face and hand) elicited anticipatory brain activity whose sources were located in their corresponding sections of the sensorimotor cortex, thus revealing a pattern of semantic somatotopy (Pulvermüller et al., 2005; Kemmerer, 2015). Semantically constrained contexts led to SRPs irrespective of whether they had a positive or negative meaning, thus predicting a specific lexical item with high probability. Intriguingly, predictive sensorimotor activation was more widespread in negated than in affirmative High-constraint sentences, which is consistent with predictive processing *of multiple semantic alternatives* during the former. Furthermore, compared with affirmative sentence contexts, negated ones led to predictive activation in the temporoparietal junction, temporal pole and the medial prefrontal cortex.

The hypothesis that multiple semantic alternatives are processed in the prediction of negated propositions is also consistent with the pattern of N400 responses to the congruent and incongruent critical words. Indeed, the typical pattern of a relatively enhanced N400 to semantically incongruous endings (Kutas and Federmeier, 2011) was only found for incongruous target words in affirmative sentence contexts. The Low-constraint contexts produced similar N400s for the semantically-related and -unrelated target words, as they were both unpredictable. Importantly, minimal N400s were found in all High-constraint negative contexts, even for unexpected target words, thus suggesting that untypical action-semantic sentence endings were at some level expected in this type of context.

We focused here on sentences in which the predicted symbols were action verbs with semantic relationship to overt bodily actions typically performed by human subjects, and it may be that aspects of our findings are specific, or most pronounced, for this lexical type. Furthermore, to avoid overlap of brain responses elicited by sentence context and expected semantic types, we introduced a 1.5 s pause before the critical word, which may be seen as making language use in this experiment somewhat ‘unnatural’. In this view, the pause could lead to experiment-specific strategic processes, thus suggesting prudence in generalizing our results to natural language use. However, at least three arguments speak against this possibility. First, pauses naturally and frequently occur in normal conversation (Fernald et al., 1989); second, participants were listening to sentences passively while watching a silent movie, being instructed to ignore any verbal input, which works against an explicit strategy of stimulus analysis; third, the comparison between the SRP mean amplitude extracted from the first and the last trials failed to indicate neurophysiological changes, although in case of dependence of neurophysiological responses on experiment-specific strategies one would expect development of such strategies/responses across the experiment. Still, we cannot exclude that specific features of our experiment play a role in eliciting the predictive brain responses observed and future work is therefore necessary to confirm and extend the present results. However, major features of the observed SRP dynamics are explainable by predictability and negation alone. For example, when the negation was placed at the beginning of the sentences, as in “*I do not take the pen and I* <u>*write*</u>”, we observed a drop in the ability to predict the final word, “*write*” (**Figure 1b**), and no anticipatory activity before the word (**Figure 2a**). However, when the negation was placed just before the critical word (as in “*I take the pen but I do not* <u>*write*</u>”) the participants were still able to predict the congruent critical words just as in the affirmative sentence conditions (i.e. “*I take the pen and I* <u>*write*</u>”) (**Figure 1b**). Coherently, in these predictable situations we observed similar SRPs whose latencies, scalp distributions and negative polarities are consistent with an RP (**Figure 2a,c**).

SRP as an index of semantic prediction

A broad range of studies on semantic processing investigated the N400 component (Kutas and Federmeier, 2011) to draw conclusions on the pre-activation of lexico-semantic circuits during sentence comprehension (Van Berkum et al., 2005). However, as the N400 follows the critical predicted/unpredicted word, it does not directly reflect the build-up of activation related to prediction, but rather the match or mismatch between such predictions and the (expected or unexpected) critical stimulus. For example, De Long and colleagues (2005) demonstrated that the sentence "*The day was breezy so the boy went outside to fly an airplane*" elicited larger N400 responses to the final article "*an*" and noun "*airplane*" as compare to the same sentence presented with the expected ending composed by the article "*a*" and "*kite*". The larger N400 elicited by the last noun (i.e. *airplane*) could be explained both in terms of word pre-activations and semantic integration process, because the two nouns (i.e. *airplane* and *kite*) differ in meaning. However the two articles "*a*" and "*an*" are meaningfully equivalent thus revealing that the N400 responses in this case would imply that the listeners have already formed the expectation for "*kite*" than for "*airplane*" (Otten et al., 2007). Although these results show a brain index of semantic anticipation in sentence understanding, they still report responses following items that had first been predicted at an earlier stage – as even the determiners 'a' or 'an' were predictable based on the preceding sentence fragment.

Few studies address the direct neurophysiological correlates of predictions preceding expected language units. For example, Pulvermüller and coworkers (2006) reported MEG activity indexing the point in time of whole-word recognition before the end of spoken words, and Söderström and colleagues (2016) reported that brain activity elicited by word-initial phonemes indicate the predictability of the unfolding words. Dikker and Pylkkanen (2013) found brain correlates of the predictability of nouns upon corresponding object picture presentation, although picture makeup and repetition represent possible confounds of this work. Fruchter and colleagues (2015) found brain activation to adjectives related to their predictive information on subsequent nouns and localized the origin of this predictive activity in anterior temporal cortex. Maess and colleagues (2016) found brain responses reflecting the predictability of nouns upon stimulus verbs. On the background of these innovative studies of linguistic-predictive brain activity, an important novel finding of the present work was that, before predicted words appeared, anticipatory patterns of brain activity and their underlying source constellations *revealed aspects of the meaning of the expected words and sentence endings*. This bolsters the semantic character of the SRP. The word-related topography modulation was observed at the end of the RP curves when precentral gyrus activation and somatotopic differences are normally present in RP studies of voluntary movement tasks (Ball et al., 1999; Weilke et al., 2001). Furthermore, at the same latency the neurophysiological source analysis confirmed the hypothesis of different cortical generators between the *face-* and *hand-related* semantic expectations. As in earlier work (Hauk et al., 2004; Pulvermüller and Fadiga, 2010), semantically-related somatotopic activity was observed, that is, the expectation of *hand-related* words brought about greater activation in hand motor areas as compare with expectations of *face-related* words and, vice versa, greater activation within face motor areas when participants expected *face-* as compare with *hand-related* words (**Figure 2a,b; Table 2**).

Negative predictable contexts lead to processing multiple semantic alternatives

Previous studies of negation differed in their results. Fischler and coworkers (1983) found that N400 responses depended on semantic relationships between context and critical words, but affirmative or negated sentence meaning was only reflected at a later stage. However, recent investigations (Nieuwland and Kuperberg, 2008) showed larger N400 for false as compared with true statements, independent of negation (along with a further influence of pragmatic factors). Our present SRP sources confirm an early onset of sentential negation processing, possibly even before the sentence final word. In our results, unpredictable negated sentences elicited substantial N400s, which were similar to those obtained when semantic expectations were violated (incongruent AHC condition). Therefore, the predictability and negation factors are both necessary to explain N400 dynamics following the critical words.

Simultaneous processing of alternative action hypotheses offers an explanation why, in negated High-constraint contexts, SRP sources were more widespread and N400s were generally minimal. Negation-related SRPs were due to larger sources not only in motor systems (see below) but also in temporoparietal junction, temporal pole and the medial prefrontal cortex.

These regions are part of the theory-of-mind (TOM) network (Saxe et al., 2004; Amodio and Frith, 2006). Although, temporal poles and the left inferior posterior temporal cortex are frequently discussed as semantic hubs (see, for example, Patterson et al., 2007), the dorsal medial prefrontal cortex is not a semantic area in this sense. Regarding parietal cortex, particularly the temporoparietal junction (TPJ), opinions are mixed, with some authors (Binder and Desai, 2011) attributing a general semantic role and others (Patterson et al., 2007) denying it. Therefore, we believe that the set of areas found active in negation processing is best characterized as similar to the TOM network, although it includes established 'semantic areas'. Our suggestion that multiple action-semantic alternatives are processed in predictable negated contexts is consistent with a greater engagement of TOM networks and semantic systems of the human brain, including motor areas.

Previous studies reported diminished motor activity following *action-related* words in negative contexts (Tettamanti et al., 2008; Tomasino et al., 2010; Liuzza et al., 2011; Aravena et al., 2012). Our present results offer a possibility why this was so: because, in some of the experiments, the action hypotheses had already been present in the predictive baselines, the neuronal circuit of the subsequent action concept was already primed so that reduced semantic activity, manifest, in part, in motor systems, was observed in response to word presentation. In a previous study, we showed that motor cortex activation to action words is indeed greatly reduced in contexts where these words are predictable so that their neuron circuits have been primed semantically by context (Grisoni et al., 2016). The current results shed new light on the brain mechanisms of semantic processing as they draw attention to the importance of the interplay between predictive processes and prediction resolution, here directly reflected by SRP and N400 responses, respectively. Furthermore, they demonstrate the importance of the specific and complementary roles of modality-specific and modality-general brain systems in sentence-level meaning processing.

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Tables

Conditions	Sentence fragments	SRP	Expected/Unexpected critical words	N400
AHC	I take the pen and I	+	**write/eat**	**-/+**
	I find the broom and I	+	**sweep/smoke**	**-/+**
	I take some grapes and I	+	**eat/write**	**-/+**
	I find a cigarette on the desk and I	+	**smoke/sweep**	**-/+**
NHC	I take the pen but I do not	+	**write/eat**	**-/-**
	I find the broom but I do not	+	**sweep/smoke**	**-/-**
	I take some grapes but I do not	+	**eat/write**	**-/-**
	I find a cigarette on the desk but I do not	+	**smoke/sweep**	**-/-**
NLC	I do not take the pen and I	-	**write/eat**	**+/+**
	I do not find the broom and I	-	**sweep/smoke**	**+/+**
	I do not take some grapes and I	-	**eat/write**	**+/+**
	I do not find a cigarette on the desk and I	-	**smoke/sweep**	**+/+**

Table 1 Experimental conditions and example stimuli. Each of the three context conditions, Affirmative High-constraint (AHC), Negative High-constraint (NHC), and Negative Low-constraint (NLC), contained sentence fragments specifying hand or leg actions. The second column contains examples of the sentence fragments, which elicit different expectations of subsequent critical words. The next column shows whether the context of the sentence fragments licensed strong predictions on specific critical words, in which case a Semantic Readiness Potential, SRP, was expected (+). If not, no SRP was predicted (-). The sentences were completed with either Expected or Unexpected critical words, which were either *face-* or *hand-related* and thus either body-part-congruent with the fragments or not. The last column shows whether an enlarged N400 was expected (+) or not (-), depending on the critical word presented.

	x	y	z	t values (peak-level)	Number of voxels	P values (FWE-corrected)	Brodmann areas	Cortical areas
fMRI: Motor localizer results: Lips movement > baseline	-54	-10	39	12.39		p < 0.001	4	Ventral Pre- and Post-central gyrus
fMRI: Motor localizer: Fingers movement > baseline	-36	-18	62	16.66		p < 0.001	4	Dorsal Pre- and Post-central gyrus
t-test against zero on sources from the ERP obtained by collapsing all the High-constraint conditions First Time window: -80 -40ms before word onset	52	-6	-30	8.87	4039	p = 0.015	20	Anterior temporal lobe
	-44	16	-26	7.62	3827	p = 0.016	38	Anterior temporal lobe
	-18	50	-16	6.25	3288	p = 0.017	11	Orbitofrontal cortex
	4	56	-14	6.13	580	p = 0.036	11	Orbitofrontal cortex
	-46	-50	-14	4.52	1462	p = 0.027	20	Posterior temporal lobe
	44	44	14	4.15	80	p = 0.046	45	Posterior inferior prefrontal cortex
t-test against zero on sources from the ERP obtained by collapsing all the High-constraint conditions Second Time window: last 20ms before word onset	-48	-12	-30	8.61	6093	p = 0.007	20	Anterior temporal lobe
	52	-10	-32	8.14	3187	p = 0.014	20	Anterior temporal lobe
	42	36	-2	6.45	7343	p = 0.005	47	Posterior inferior prefrontal gyrus
	16	-94	14	5.19	2677	p = 0.016	18	Occipital cortex
	-30	24	40	5.06	2013	p = 0.019	9	Dorsolateral prefrontal cortex
	46	-28	46	5.00	1100	p = 0.026	3/4	Pre- and post-central gyrus
	-44	-30	48	4.06	1137	p = 0.026	3	Dorsolateral Pre- and Post-central gyrus
	-42	40	2	4.71	476	p = 0.035	45	Inferior prefrontal cortex
	38	-78	28	4.32	161	p = 0.042	39	Parietal lobe
	56	-46	-10	4.21	67	p = 0.045	20	Posterior temporal lobe
	-40	-76	28	4.16	167	p = 0.042	39	Parietal lobe
face- > hand-related expected semantic types **ROIs**	-50	-22	44	4.71	1212	p = 0.021	4	Pre-central gyrus
	-42	-22	50	4.19	508	p = 0.031	3	Post-central gyrus
***face- > hand-related* expected semantic types ROIs**	-24	-24	66	4.77	99	p = 0.042	4	Pre-central gyrus
Whole brain contrast: AHC > NHC	-40	58	4	4.17	157	p = 0.027	46	Inferior frontal gyrus
Whole brain contrast: NHC > AHC	44	-22	-26	9.29	6935	p < 0.001	20	Temporal pole
	-52	-22	-26	9.29	4650	p < 0.001	20	Temporal pole
	52	-42	36	6.00	391	p = 0.016	48	Temporoparietal junction (TPJ)
	32	16	38	5.70	657	p = 0.010	46	Dorsolateral prefrontal cortex
	-50	-46	34	5.53	152	p = 0.027	48	Temporoparietal junction (TPJ)
	16	30	52	5.43	124	p = 0.029	8	Medial frontal cortex
Brodmann areas 3, 4 and 6 restricted contrast: NHC > AHC	12	30	58	5.74	1431	p = 0.014	6	Pre-central gyrus
	34	4	34	5.38	117	p = 0.039	6	Pre-central gyrus
	-8	28	44	4.84	339	p = 0.031	6	Pre-central gyrus
	-50	4	36	4.47	125	p = 0.039	6	Pre-central gyrus
	-54	-24	56	4.25	180	p = 0.036	3	Post-central gyrus

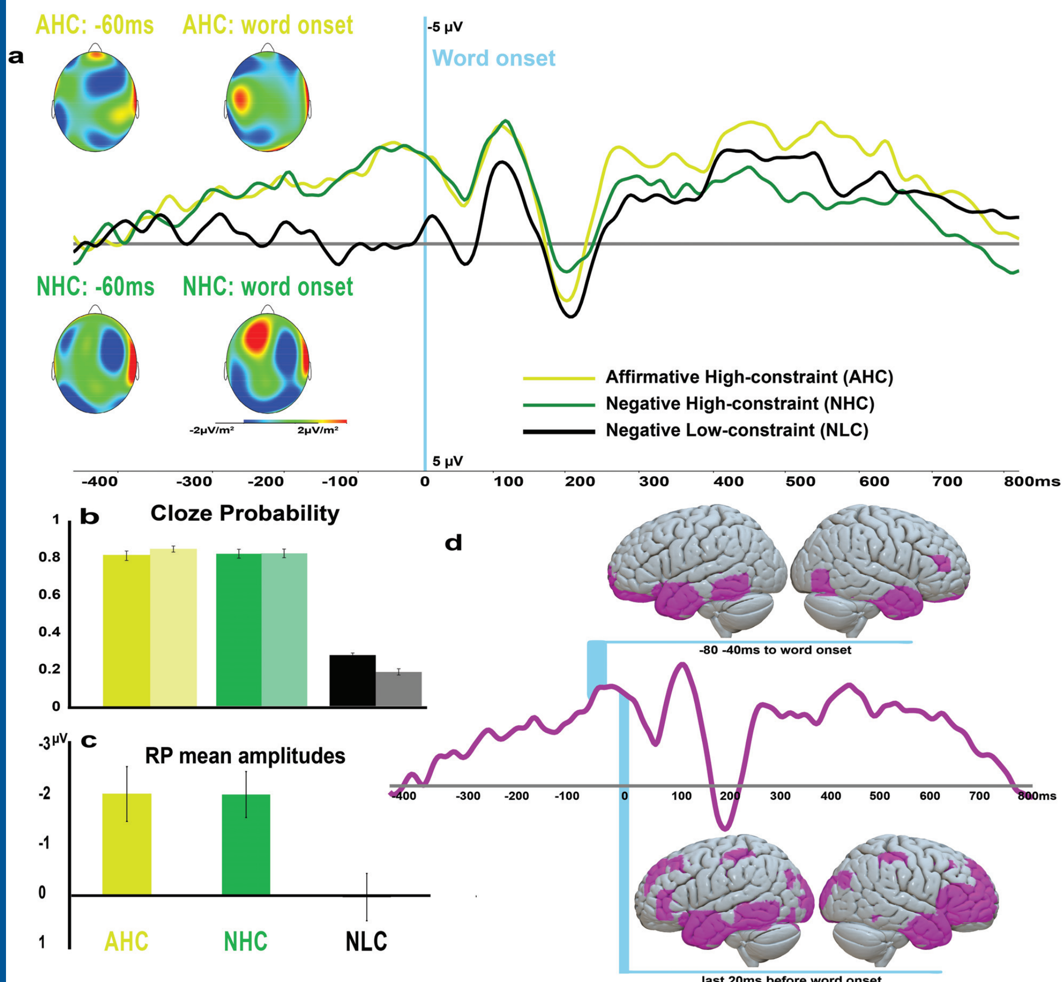
Table 2 fMRI and source analysis results. For all significant contrasts calculated on the fMRI results and the cortical sources of the first and second SRP time intervals and for all significant clusters, the table displays the MNI coordinates of the voxel with highest t-value, its t-value, the number of significant voxels per each significant cluster, FEW-corrected P-value, and the Brodmann area labels where the 'peak voxel' was found, along with a description of the cortical area where the active cluster was located.

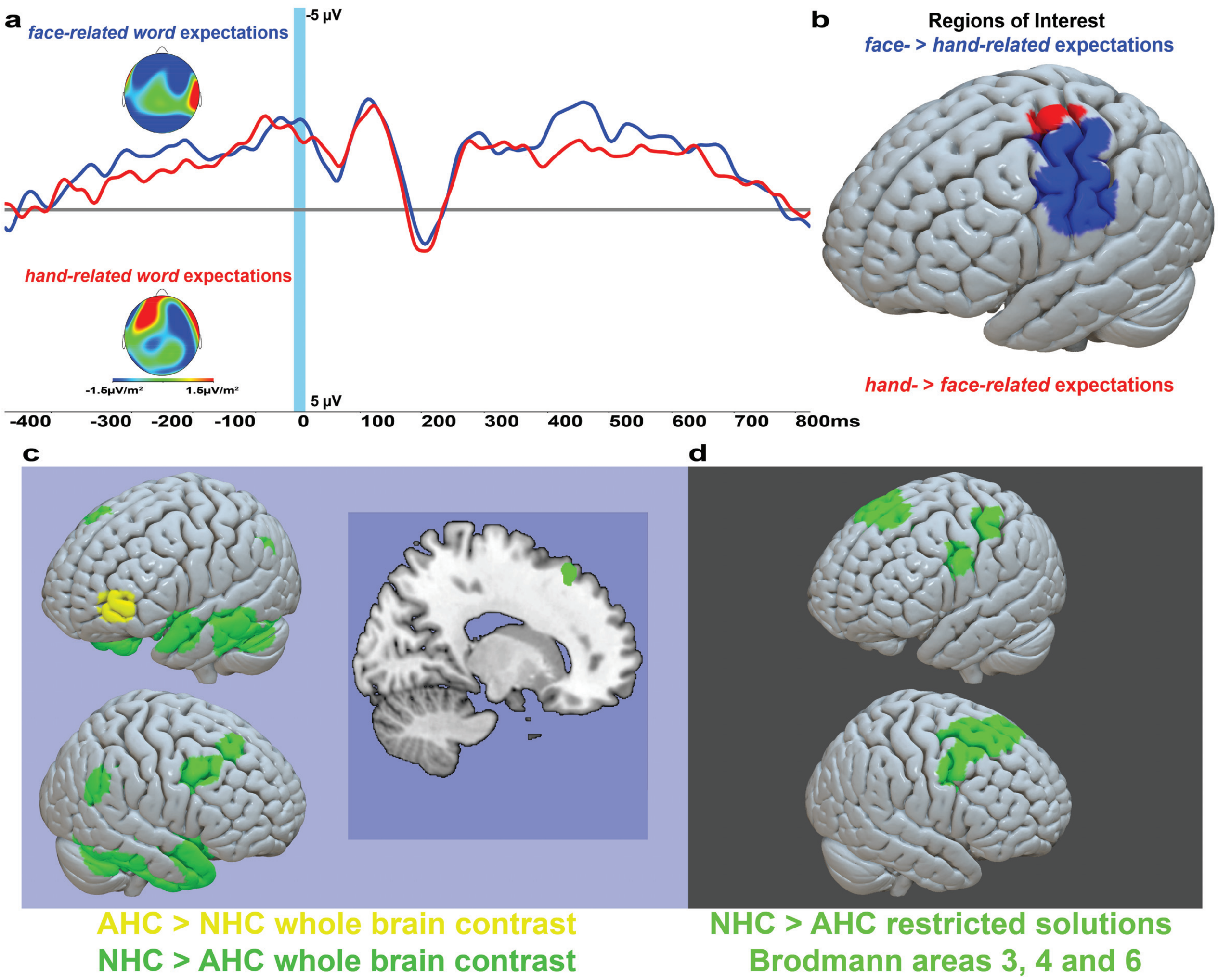
Figure captions

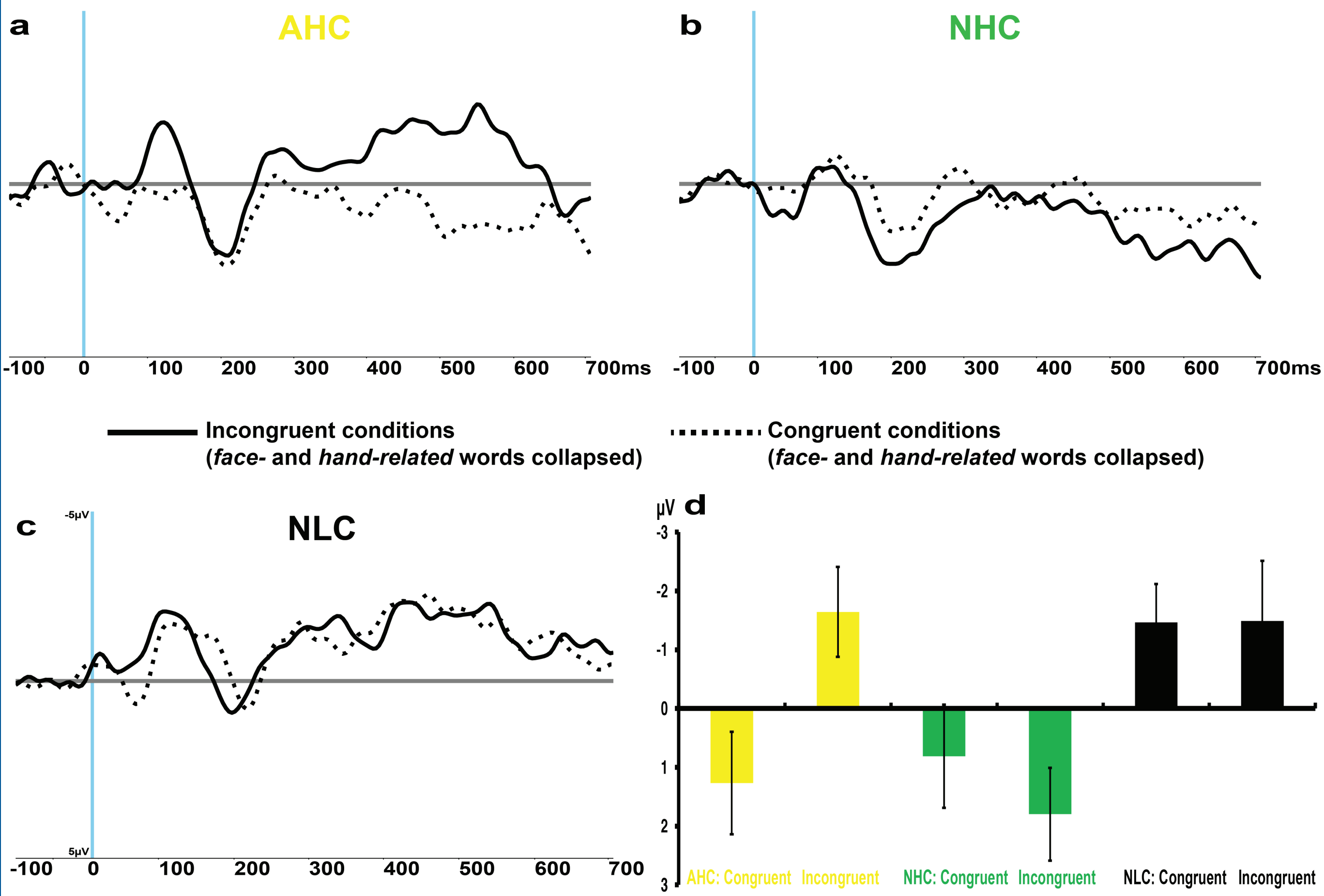
Figure 1 Cloze Probability and electrophysiological results. a Event-related potentials elicited in the three context (AHC: **yellow**, NHC: **green** and NLC: **black**) as the average of the fronto-central electrodes (FC1, FC2 FCz, FC3, FC4, C1, C2, Cz, C3, C4, CP1, CP2, CPz, CP3, CP4). **b** Cloze probability evaluation of the experimental sentences. To estimate the predictability of our sentences, we followed established cloze probability tests taking the frequency with which the EEG and an independent group of participants reported, at least once, the word presented in the semantically congruent condition. From left to right, Affirmative High-constraint (AHC, **yellow: opaque for EEG participants, transparent for an independent sample**), Negative High-constraint (NHC, **green: opaque for EEG participants, transparent for an independent sample**) and Negative Low-constraint (NLC, **black: opaque for EEG participants, transparent for an independent sample**) contexts (mean and SEM). In panel **c** the RP mean amplitude (μV) extracted from the last 100ms before word onset are plotted. Panel **d** shows the RP collapsed across the High-constraint conditions (HC: **violet**) together with the corresponding sources estimated at two different latencies light blue highlighted (i.e. from 80 to 40ms before word onset, and in the last 20ms before word onset). All indicated clusters were significantly active (t-tests, $p < 0.05$, whole brain FWE correction).

Figure 2 Semantic readiness potential (SRP): predictive brain activity for *face-* and *hand-related* words. a SRP curves in anticipation of *face-* (**blue**) and *hand-related* (**red**) words (High-constraint contexts collapsed). The light blue window shows the last 20ms before word onset. **B** Source analysis results comparing predictive brain activity for *face-* and *hand-related* words within the sensorimotor cortex (see **Methods**). Ventral regions (**blue**) revealed a significant contrast *face-* > *hand-related* word predictions, whereas dorsolateral sources showed the opposite contrast (**red**). Panel **c** shows statistically significant clusters obtained after whole brain FWE correction Affirmative High-constraint (AHC) > Negative High-constraint (NHC) (**yellow**) and Negative High-constraint (NHC) > Affirmative High-constraint (AHC) (**green**). The latter contrast (**green**) showed activity in TOM areas and (i.e. temporal lobes, temporoparietal junction, frontal and medial frontal cortex) as well as – see panel **d** – widespread sensorimotor system activity.

Figure 3 N400 results for the AHC, NHC and NLC contexts. Congruent (dotted line) and incongruent (solid line) conditions in AHC (**top left**), NHC (**top right**) and NLC (**bottom left**) are plotted as the average of three midline electrodes used for statistical comparisons (FCz, CPz, POz). The panel on the **bottom right** shows the statistically significant interaction of the factors Context and Congruency (mean and SEM; from left to right Affirmative High-constraint (**yellow**), Negative High-constraint (**green**) and Negative Low-constraint (**black**) contexts).


a
AHC: -60ms
AHC: word onset
NHC: -60ms
NHC: word onset
-2μV/m²
2μV/m²
-5 μV
Word onset
5 μV
Affirmative High-constraint (AHC)
Negative High-constraint (NHC)
Negative Low-constraint (NLC)
-400 -300 -200 -100 0 100 200 300 400 500 600 700 800ms
b
Cloze Probability
1 0.8 0.6 0.4 0.2 0
c
RP mean amplitudes
-3μV -2 -1 0 1
AHC
NHC
NLC
d
-80 -40ms to word onset
-400 -300 -200 -100 0 100 200 300 400 500 600 700 800ms
last 20ms before word onset


a
face-related word expectations
-5 µV
hand-related word expectations
-1.5µV/m²
1.5µV/m²
5 µV
-400
-300
-200
-100
0
100
200
300
400
500
600
700
800ms
b
Regions of Interest
face- > hand-related expectations
hand- > face-related expectations
c
d
AHC > NHC whole brain contrast
NHC > AHC whole brain contrast
NHC > AHC restricted solutions
Brodmann areas 3, 4 and 6


a
AHC
-100
0
100
200
300
400
500
600
700ms
b
NHC
-100
0
100
200
300
400
500
600
700ms
Incongruent conditions
(*face-* and *hand-related* words collapsed)
Congruent conditions
(*face-* and *hand-related* words collapsed)
c
-5µV
NLC
5µV
-100
0
100
200
300
400
500
600
700
µV
d
-3
-2
-1
0
1
2
3
AHC: Congruent
Incongruent
NHC: Congruent
Incongruent
NLC: Congruent
Incongruent