Neural evidence for the prediction of animacy features during language comprehension: Evidence from MEG and EEG Representational Similarity Analysis

Lin Wang[1,2], Edward Wlotko[2,3], Edward Alexander[1,2], Lotte Schoot[1,2], Minjae Kim[2,4], Lena Warnke[1,2], Gina R. Kuperberg[1,2]

1 Department of Psychiatry and the Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, MA, 02129, USA

2 Department of Psychology, Tufts University, Medford, MA, 02155, USA

3 Moss Rehabilitation Research Institute, Elkins Park, PA, 19027, USA

4 Psychology Department, Morrissey College of Arts and Sciences, Boston College, Chestnut Hill, MA, 02467, USA

Corresponding author email address: wanglinsisi@gmail.com; gkuperberg@mgh.harvard.edu

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Abstract

It has been proposed that people generate probabilistic predictions at multiple levels of linguistic representation during language comprehension. Here we used Magnetoencephalography (MEG) and Electroencephalography (EEG) in combination with Representational Similarity Analysis (RSA) to seek neural evidence for the prediction of animacy features. In two studies, MEG and EEG activity was measured as participants read three-sentence scenarios in which the verbs in the final sentences constrained for either animate or inanimate semantic features of upcoming nouns. The broader context constrained for either a specific noun or for multiple nouns belonging to the same animacy category. We quantified the spatial similarity pattern of the brain activity measured by MEG and EEG following the verbs until just before the presentation of the nouns. We found clear and converging evidence across the MEG and EEG datasets that the spatial pattern of neural activity following animate constraining verbs was more similar than the spatial pattern following inanimate constraining verbs. This effect could not be explained by lexical-semantic processing of the verbs themselves. We therefore suggest that it reflects the inherent difference in the semantic similarity structure of the *predicted* animate and inanimate nouns. Moreover, the effect was present regardless of whether it was possible to predict a specific word on the basis of the prior discourse context. This provides strong evidence for the prediction of coarse-grained semantic features that goes beyond the prediction of individual words.

Significant statement

Language inputs unfold very quickly during real-time communication. By predicting ahead, we can give our brains a “head-start”, so that language comprehension is faster and more efficient. While most contexts do not constrain strongly for a specific word, they do allow us to predict some upcoming information. For example, following the context, "they cautioned the…”, we know that the next word will be animate rather than inanimate (we can caution a person, but not an object). Here we used EEG and MEG techniques to show that the brain is able to use these contextual constraints to predict the animacy of upcoming words during sentence comprehension, and that these predictions are associated with specific spatial patterns of neural activity.

Introduction

It has been proposed that probabilistic prediction is a fundamental computational principle underlying language comprehension. Evidence for this hypothesis comes from the detection of anticipatory neural activity prior to the appearance of strongly predicted incoming words (e.g. Wicha et al., 2004; Piai et al., 2016; Wang et al., 2018). During natural language, however, contexts that predict specific words appear relatively infrequently (Luke and Christianson, 2016). Therefore, for prediction to play a major role in language processing, comprehenders must be able to use contextual constraints to predict features that characterize multiple upcoming inputs. In the present study, we ask whether comprehenders are able to use the constraints of verbs to predict semantic features associated with the *animacy* of upcoming nouns during word-by-word discourse comprehension.

The ability to distinguish between animate and inanimate entities is fundamental to human cognition (Caramazza and Shelton, 1998; Nairne et al., 2017) and to the structure of language (Dahl, 2008). Verbs can constrain for the animacy of their arguments (McCawley, 1968; Jackendoff, 1993), and these constraints can lead to anticipatory behavior during online language comprehension (Altmann and Kamide, 1999). Moreover, a larger event-related potential (ERP) response (the N400) is evoked by nouns that mismatch (versus match) these constraints (Paczynski and Kuperberg, 2011, 2012; Szewczyk and Schriefers, 2011), and neural effects to mismatching inputs can be detected even before the animacy features of upcoming arguments become available (Szewczyk and Schriefers, 2013). Here we sought direct neural evidence for the prediction of animacy features in the absence of any mismatching or matching bottom-up input, by exploiting an inherent difference in the *semantic similarity structure* of animate and inanimate nouns.

Animate entities share more semantic features, which are more strongly intercorrelated, than inanimate entities (McRae et al., 1997; McRae et al., 1999; Garrard et al., 2001; Zannino et al., 2006). For example, the animate words, “swimmer” and “pilot”, share more co-occurring semantic features (e.g. <can move>, <can breathe>, <sentient>) than the inanimate words, “paper” and “water”, which have more distinct features (e.g. <thin> for “paper”, <drinkable> for “water”). In the brain, semantic features are thought to be represented within widely distributed networks (Martin and Chao, 2001; Thompson-Schill, 2003). Thus, difference in the internal semantic similarity structures of *animate* and *inanimate* concepts can give rise to differences in the spatial similarity patterns of neural activity associated with their processing. These differences can explain specific patterns of category-specific deficits observed in patients with non-focal neuropathologies (Devlin et al., 1998; Tyler and Moss, 2001; McRae and Cree, 2002; Taylor et al., 2011). They can also be detected using a technique known as Representational Similarity Analysis (RSA) (Kriegeskorte et al., 2008a).

RSA has been used to discriminate between *animate* and *inanimate* entities with fMRI and, more recently, with MEG and EEG (Sudre et al., 2012; Carlson et al., 2013; Cichy et al., 2014), which can track changes in spatial similarity patterns over time. In the present study, we use RSA together with both MEG and EEG, which yield complementary information about underlying neural activity (Hämäläinen et al., 1993; Cichy and Pantazis, 2017), to ask whether, during online language comprehension, features linked to the *animacy* of an upcoming noun can be predicted on the basis of a preceding verb that constrains either for an *animate* or *inanimate* direct object noun (see Table 1). If comprehenders are able to use these animacy constraints to predict semantic features associated with the upcoming noun, then the spatial pattern of neural activity following *animate constraining* verbs should be more similar than following *inanimate constraining* verbs, and this effect should appear *before* the onset of the noun. Moreover, if such predictions are generated irrespective of predicting specific words, this effect should be just as large following *low constraint* discourse contexts as following *high constraint* discourse contexts.

Materials & Methods

Overall structure of experiments and analysis approach

We carried out two studies using the same experimental design and overlapping sets of stimuli. In the first study, we collected MEG and EEG data simultaneously in 32 participants. In the second study, we collected EEG data in 40 different participants. We analyzed the MEG data and the EEG data separately. For the EEG analysis, we combined the EEG data from the first and second studies to maximize statistical power (n=72).

In this Methods section, we first introduce the experimental design and stimuli, which were used in both the MEG-EEG study and the EEG-only study. Second, we report the participants and overall procedures for each of the two studies. Third, we report MEG data acquisition and preprocessing (for the first MEG-EEG study), and EEG data acquisition and preprocessing (for both the first MEG-EEG study and the second EEG-only study). Finally, we describe the spatial similarity analysis, which was the same for the MEG and the (combined) EEG data.

Experimental design and stimuli

Experimental design

In both the MEG-EEG study and the EEG-only study, stimuli were three-sentence scenarios (Table 1). The first two sentences introduced a discourse context, and the final sentence began with an adjunct phrase of 1-4 words, followed by a pronominal subject that referred back to a protagonist introduced in the first two sentences, followed by a verb. Following the verb, there was a determiner, a direct object noun, followed by three additional words to complete the sentence. The verb in the third sentence (referred to as the *critical verb*) varied in whether it constrained for an *animate* direct object noun (*animate constraining:* 50%, e.g. “cautioned the…”) or an *inanimate* direct object noun (*inanimate constraining:* 50%, e.g. “unfolded the…”). In addition, the lexical constraint of full discourse context (the combination of the first two sentences and the first few words of the third sentence including the verb and the determiner) varied such that it constrained for a single word (*high discourse constraint*: 50%, e.g. “The lifeguards received a report of sharks right near the beach. Their immediate concern was to prevent any incidents in the sea. Hence, they cautioned the…”), or for no specific single word (*low discourse constraint*, e.g. “Eric and Grant received the news late in the day. They mulled over the information, and decided it was better to act sooner rather than later. Hence, they cautioned the…”). This crossing of Verb animacy constraint (*animate constraining*, *inanimate constraining*), and Discourse constraint (*high discourse constraint*, *low discourse constraint*) gave rise to the four conditions relevant to the present study.

Following the verb, a direct object noun either confirmed (e.g. “trainees”) or violated (e.g. “drawers”) the verb’s animacy constraint, rendering the scenarios plausible or implausible. In the present study, however, we focus on activity from the onset of the verb until just *before* the onset of the direct object noun.

Insert Table 1 here

Construction of scenarios

In order to construct these scenarios, we began with a large set of preferentially transitive verbs. We first established their animacy constraints as well as their lexical constraints in minimal contexts by carrying out an offline cloze norming study, described below. Then, on the basis of these norms, we selected a subset of *animate* and *inanimate* constraining verbs, which, in these minimal contexts, had low lexical constraint for the following noun. We then wrote *high discourse constraint* and *low discourse constraint* contexts around each verb. We quantified the lexical constraint of each discourse context for the following noun (the first two sentences plus the third sentence until after the determiner) with a second cloze norming study, described below.

Cloze norming studies

In both cloze norming studies, participants were recruited through Amazon Mechanical Turk. They were asked to complete each context with the first word that came to mind (Taylor, 1953), and in an extension of the standard cloze procedure, to then provide two additional words that could complete the sentence (see Schwanenflugel and LaCount, 1988; Federmeier et al., 2007). Responses were excluded if the first language learned was anything other than English or if there were any self-reported psychiatric or neurological disorders. Responses were also excluded for any participants who failed to follow instructions ("catch" questions were used as periodic attention checks).

Cloze norming study 1: To select the verbs based on their animacy and lexical constraints in minimal contexts

We began with a set of 617 transitively-biased verbs, compiled from various sources including Levin (1993) and materials from previous studies conducted in our laboratory (Paczynski and Kuperberg, 2011, 2012). Verbs with log Hyperspace Analogue to Language (HAL) frequency (Lund and Burgess, 1996) of two standard deviations below the mean (based on English Lexicon Project database: Balota et al., 2007) were excluded. For each verb, we constructed a simple active, past tense sentence stem that consisted of only a proper name, the verb, and a determiner (e.g., "Harry cautioned the…"). These sentences were divided into six lists in order to decrease the time demands on any individual participant during cloze norming. Between 89 and 106 participants (depending on list) who met inclusionary criteria provided completions for each verb.

For each verb, we identified the best completion of the sentence context (i.e. the most common first noun produced across all participants), and, based on the animacy of these nouns, we categorized the verb as either *animate constraining* or *inanimate constraining*. We also tallied the number of participants who produced this best completion in order to calculate the lexical constraint of the verbs for specific upcoming nouns in these minimal contexts. To generate the final set of discourse stimuli, we selected 175 verbs (88 *animate constraining* and 87 *inanimate constraining*), all with lexical constraints of lower than 24%.

Cloze norming study 2: Constraint of the entire discourse contexts for upcoming nouns

For each of the *animate constraining* and *inanimate constraining* verbs, we wrote high constraint and low constraint two-sentence contexts that, in combination with the first few words of the third sentence, the verb, and the determiner aimed to constrain for a single upcoming word (*high discourse constraint)* or for multiple possible upcoming words (*low discourse constraint)*. We then carried out a second cloze norming study of these discourse contexts to quantify these discourse constraints. For this study, the *high discourse constraint* and *low discourse constraint* contexts were pseudorandomly divided into two lists such that each list contained only one of the two contexts associated with each verb. The two lists were then divided into thirds to decrease time demands on any individual participant during cloze norming. Between 51 and 69 participants who met inclusionary criteria provided completions for each scenario. The mean lexical constraint of the *high discourse constraint* contexts was 67.80% (SD: 15.00%) and the mean lexical constraint of the *low discourse constraint* context was 21.56% (SD: 12.00%), and this differed significantly between the two conditions, $t_{(698)} = 45.01$, $p < 0.001$.

Distribution of stimuli into lists

The stimuli were then divided to lists, with each list containing (approximately) 50% *animate constraining* verbs and 50% *inanimate constraining* verbs, distributed evenly across the *high discourse constraint* and the *low discourse constraint* contexts. The lists were constructed so that the same verb was not combined with the same discourse context more than once, but across lists, all critical verbs were combined with both *high discourse constraint* and *low discourse constrain*t contexts. Although the present study focused on activity prior to the onset of the direct object noun, we constructed scenarios such that the subsequent direct object noun either confirmed the animacy constraints of the verb (and so the scenario was plausible) or disconfirmed the animacy constraints of the verb (and so the scenario was anomalous). The lists were constructed so that each participant viewed 50% plausible scenarios (25% of these plausible scenarios contained lexically predicted nouns in *high discourse constraint contexts*), and 50% anomalous scenarios. Thus, a scenario was just as likely to be plausible following a *high discourse constraint* context as following a *low discourse constraint* context.

In the first MEG-EEG study, the stimuli constituted 700 scenarios, which were divided into four lists, with each list containing 200 scenarios. Within each list, 101 scenarios contained *animate constraining* verbs and 99 scenarios contained *inanimate constraining* verbs. Since there were overall 175 unique verbs (88 *animate constraining* and 87 *inanimate constraining*), this meant that a small number of verbs in the third sentence were repeated: 13 out of 101 *animate constraining* verbs and 12 out of 99 *inanimate constraining* verbs.

In the second EEG-only study, we included a subset of 600 scenarios, which were divided into five lists. Each list contained 160 scenarios, with no verb being repeated in any of the lists (80 unique *animate constraining* and 80 unique *inanimate constraining* verbs). A detailed description of the precise counterbalancing scheme can be found in Kuperberg et al., (2019).

Quantification of the semantic and lexical similarity structures of the verbs

Semantic similarity structure of the animate constraining and the inanimate constraining verbs

In order to be able to infer that any difference in the neural pattern of spatial similarity produced following the *animate* and *inanimate constraining* verbs was due to the prediction of animacy features associated with the upcoming nouns for which they constrained, it was important to verify that the two groups of verbs did not differ in other aspects of their internal similarity structure. Of course, some aspects of verb meaning are inherently tied to the meaning of the arguments for which they constrain (McCawley, 1968; Jackendoff, 1993), and the goal of the present study was to ask whether such constraints were used to *predict* upcoming animacy features as the sentences unfolded in real time. However, many other aspects of a verb's meaning are not directly linked to the meaning of their arguments. In order to quantify these other components of verb meaning, we used WordNet, an English lexical database that groups words together based on their semantic relations (Miller et al., 1990), and that has been integrated in the Natural Language Toolkit (NLTK) (Loper and Bird, 2002). In WordNet, verbs are organized into hierarchies based on their semantic relations (Fellbaum, 1990), such as specificity in manner (e.g. walking – strolling), entailments (e.g. sleeping – snoring), causation (e.g. drop – break) and antonymy (e.g. coming – going). By examining the hierarchical structure of this network, the semantic similarity between different verbs can be quantified.

When examining the WordNet hierarchy for a given word, it is important to first consider its precise meaning in context — its so-called *sense*. For instance, the verb, "caution", has at least two senses, including (a) "warn strongly; put on guard", denoted in WordNet as Synset('caution.v.01'), and (b) "the trait of being cautious; being attentive to possible danger", denoted as Synset('caution.n.01'). Therefore, for each of our critical verbs, a native English speaker manually identified its sense within each discourse context. For example, the sense of the verb "cautioned" within the example scenario shown in Table 1 ("The lifeguards received a report of sharks right near the beach. Their immediate concern was to prevent any incidents in the sea. Hence, they cautioned …") was classified as Synset('caution.v.01'). In total, across the entire stimulus set, we identified 250 unique verb senses (113 *animate constraining*, 137 *inanimate constraining*).

We then calculated semantic similarity values between all possible pairs of verb senses within the sets of *animate constraining* and *inanimate constraining* verbs. As a measure of semantic similarity, we used a path-based approach described by Wu & Palmer (Wu and Palmer, 1994), which is known to correlate with human ratings of semantic similarity (Slimani, 2013). Wu & Palmer similarity values range between 0 and 1, with values approaching 0 indicating low similarity, and a value of 1 indicating identical concepts. We stored these pairwise Wu-Palmer semantic similarity values in a 250 by 250 symmetric semantic similarity matrix, with rows and columns indexing the individual verbs' senses, see Figure 1A. Examination of this matrix did not reveal any clear difference in the internal semantic similarity structure between the *animate constraining* verbs (top-left: semantic similarity values for verb senses, 1 to 113: 113*112/2 = 6328 pairs) and the *inanimate constraining* verbs (bottom-right: semantic similarity values for verb senses, 114 to 250: 137*136/2 = 9316 pairs).

To test this statistically, we carried out a permutation-based statistical test on these pairwise similarity values, after excluding the values of 1s along the diagonal line. We extracted the Wu & Palmer semantic similarity values for each possible pair of *animate constraining* verbs (113*112/2 = 6328 values) and took the mean value, and we did the same for each possible pair of *inanimate constraining* verbs (137*136/2 = 9316 values). We then took the difference in these means as our test statistic. After that, we randomly re-assigned the similarity values across the two groups of verbs, and re-calculated the mean difference between the two groups. We took the mean difference value for each randomization to build a null distribution. If the observed test statistic fell within the highest or lowest 2.5% of this distribution, it was considered to be significant. This test revealed that the semantic similarity among the *animate constraining* verbs (mean +/- SD = 0.24 +/- 0.09) was very slightly lower than that among the *inanimate constraining* verbs (mean +/- SD = 0.26 +/- 0.08), p = 0.04.

Insert Figure 1 here

Lexical similarity structure of the animate constraining and the inanimate constraining verbs

We also verified that the two groups of verbs did not differ in various aspects of their internal *lexical* similarity structures. To do this, we extracted the following lexical properties of each verb: length (i.e. number of letters), orthographic Levenshtein distance (OLD20, Balota et al., 2007) and log frequency (based on the SUBTLEX database Brysbaert and New, 2009). For each of these lexical variables, we calculated the absolute difference for each possible pair of *animate constraining* (88*87/2 = 3828 values) and *inanimate constraining* verbs (87*86/2 = 3741 values). As described above, we then calculated the mean value in each group and took the difference in these means as our test statistic, and tested for differences in the lexical similarity structure between the two groups of verbs using a permutation test (1000 permutations). This test showed that the internal similarity structures, based on length, orthographic neighborhood and the frequency, were matched between the *animate constraining* and *inanimate constraining* verbs, all ps > 0.07.

Quantification of the semantic and lexical similarity structures of the predicted nouns

Semantic similarity structure of animate and inanimate nouns constrained for by the verbs

Our main hypothesis rested on the assumption that predicted *animate* nouns would be more semantically similar to each other than predicted *inanimate* nouns. Obviously, we had no way of knowing precisely what nouns each participant would predict during the experiment itself, particularly in the low constraint discourse contexts. Therefore, as proxy for these semantic predictions, we took 350 (50%) of the *animate* and *inanimate* direct object nouns that participants actually viewed — those that confirmed the animacy constraints of the verbs, rendering the scenarios plausible — and quantified their semantic similarity structures. We again used WordNet in which the meaning relationships of nouns, such as super-subordinate relations (e.g. furniture – chair) and part-whole relations (e.g. chair – backrest), are organized in a hierarchical network (Miller, 1990). We again quantified their semantic similarity using Wu-Palmer semantic similarity values (Wu and Palmer, 1994).

Just as described above for the verbs, we first manually identified the sense of each noun within its preceding context for all 350 plausible scenarios (175 *animate nouns*, 175 *inanimate nouns*), resulting in 244 unique senses for the nouns (116 *animate nouns*, 128 *inanimate nouns*). We stored the Wu-Palmer semantic similarity values (Wu and Palmer, 1994) for all possible pairs of the nouns' senses in a 244 by 244 matrix, see Figure 1B. The similarity values shown at the top-left of the matrix represent the pairwise Wu-Palmer semantic similarity values for all pairs of *animate nouns* (nouns 1 to 116: 116*115/2 = 6670 pairs), and the similarity values shown at the bottom-right of the matrix represent the pairwise semantic similarity values for all pairs of *inanimate nouns* (nouns 117 to 244: 128*127/2 = 8128 pairs). This matrix suggests that the pairwise Wu-Palmer semantic similarity values for the *animate nouns* were indeed larger than those for the *inanimate nouns*. A permutation-based statistical test (1000 permutations, carried out as described above) confirmed this observation (*animate nouns*: mean +/- SD = 0.49 +/- 0.20; *inanimate nouns:* mean +/- SD = 0.29 +/- 0.19), p = 0.001).

Lexical similarity structure of the animate and inanimate nouns constrained for by their preceding verbs

Finally, it was important to rule out the possibility that any differences detected in the neural spatial similarity patterns produced by predicted *animate* and *inanimate* nouns was due to differences in the similarities in their predicted lexical features rather than their semantic features. Again, we had no way of knowing precisely what nouns each participant would predict during the experiment itself. However, we knew that 100 scenarios had *high constraint discourse constraints* and were followed by predicted nouns. Therefore, as a proxy for any lexical-level predictions, we extracted the lexical properties of the predicted nouns that followed these *high constraint discourse* contexts (the first nouns produced in the second cloze norming study described above): length (number of letters), orthographic Levenshtein distance (OLD20, Balota et al., 2007) and log frequency (Brysbaert and New, 2009). For each of these variables, we again calculated the absolute difference values between each possible pair of predicted *animate* nouns (50*49/2 = 1225 values) and predicted *inanimate* nouns (50*49/2 = 1225 values). Then we calculated the mean value in each group and took the difference as our test statistic, and tested for any difference in the lexical similarity structure between the two groups of nouns using the permutation test described above (1000 permutations). This test revealed no statistically significant differences for word length, frequency or orthographic neighborhood (all ps > 0.15).

Participants

The first MEG-EEG dataset was acquired at Massachusetts General Hospital. Written consent was obtained from all participants following the guidelines of the Massachusetts General Hospital Institutional Review Board. Thirty-three participants initially participated, but we subsequently excluded the data of one participant because of technical problems. This left a final dataset of 32 participants (16 females, mean age: 23.4 years; range 18-35 years).

The second EEG-only dataset was acquired at Tufts university. Participants gave informed consent following procedures approved by the Tufts University Social, Behavioral, and Educational Research Institutional Review Board. Data were collected from 40 participants (19 females, mean age: 21.5 years; range 18-32 years).

In both experiments, all participants were right-handed as assessed using the modified Edinburgh Handedness Inventory (Oldfield, 1971; White and Ashton, 1976). All had normal or corrected-to-normal vision and were native speakers of English with no additional language exposure before the age of 5. Participants were not taking psychoactive medication, and were screened to exclude the presence of psychiatric and neurological disorders.

Overall procedure

In both studies, stimuli were presented using PsychoPy 1.83 software (Peirce, 2007) and projected on to a screen in white Arial font on a black background, with a size that was one-tenth of the screen height. The first two sentences were each presented as a whole (each for 3900ms, 100ms interstimulus interval, ISI), followed by an intra-trial fixation (white "++++"), which was presented for 550ms, followed by a 100ms ISI. The third sentence, which contained the *animate constraining* or *inanimate constraining* verb, was presented word by word (each word for 450ms, 100ms ISI). The final word of the third sentence was followed by a pink "?" (1400ms, 100ms ISI). This cued participants to press one of two buttons with their left hand to indicate whether each discourse scenario "made sense" or not (response fingers were counterbalanced across participants). In addition, after a proportion of trials (24/200 in the MEG-EEG study; 32/160 in the

EEG-only study; semi-randomly distributed across runs), a comprehension question, referring to the immediately previous scenario, appeared on the screen (1900ms, 100ms ISI). Participants were asked to respond yes or no based on the scenario they just read. This encouraged them to attend to and comprehend the scenarios as a whole, rather than focusing only on the third sentence. Following each trial, a blank screen was presented with a variable duration that ranged from 100 to 500ms. This was then followed by a green fixation (++++) for a duration of 900ms followed by an ISI of 100ms. Participants were encouraged to blink during the green fixation period.

In both studies, stimuli were presented over several runs (in the MEG-EEG study, 200 scenarios presented over eight runs, each with 25 scenarios; in the EEG-only study, 160 scenarios presented over four runs, each with 40 scenarios). Runs were presented in random order in each participant. Before the onset of each study, a practice session was conducted to familiarize participants with the stimulus presentation and the judgment tasks.

MEG data acquisition and preprocessing

MEG data acquisition

In the MEG-EEG study, MEG data were acquired together with EEG data (the EEG setup is described below). Participants sat inside a magnetically shielded room (IMEDCO AG, Switzerland), and MEG data were acquired with a Neuromag VectorView system (Elekta-Neuromag Oy, Finland) with 306 sensors (102 triplets, each comprising two orthogonal planar gradiometers and one magnetometer). Signals were digitized at 1000Hz, with an online bandpass filter of 0.03 - 300Hz. To monitor for blinks and eye movements, Electrooculography (EOG) data were collected with bipolar recordings: vertical EOG electrodes were placed above and below the left eye, and horizontal EOG electrodes were placed on the outer canthus of each eye. To monitor for cardiac artifact, electrocardiogram (ECG) data were collected, also with bipolar recordings: ECG electrodes were placed a few centimeters under the left and right collarbones. At both EOG and ECG sites, impedances were kept at less than 30 kΩ. To record the head position relative to the MEG sensor array, the locations of three fiduciary points (nasion and two auricular), four head position indicator coils, all EEG electrodes, and at least 100 additional points were digitized using a 3Space Fastrak Polhemus digitizer, integrated with the Vectorview system. Before each run, we used the four head position indicator coils to monitor the position and orientation of the head, with respect to the MEG sensor array.

MEG data preprocessing

MEG data were preprocessed using version 2.7.4 of the Minimum Norms Estimates (MNE) software package in Python (Gramfort et al., 2014). In each participant, in each run, MEG sensors with excessive noise were visually identified and removed from further analysis. This resulted in the removal of seven (on average) out of the 306 MEG sensors. Eye-movement and blink artifacts were automatically removed using the algorithms recommended by Gramfort et al. (2013). Signal-Space Projection (SSP) correction (Uusitalo and Ilmoniemi, 1997) was used to correct for ECG artifact. Then, after applying a bandpass filter at 0.1 to 30Hz, we segmented data into -100 to 2100ms epochs (relative to verb onset). Epochs in which the range of amplitudes exceeded pre-specified cutoff thresholds (4e-10 T/m for gradiometers and 4e-12 T for magnetometers) were removed. The data of bad MEG sensors were interpolated using spherical spline interpolation (Perrin et al., 1989). Our epoch of interest for analysis was from -100 to 1100ms, relative to verb onset. On average, 85 artifact-free trials remained following the *animate constraining* verbs and 83 trials remained following the *inanimate constraining* verbs, with no statistically significant difference between the two groups: $F_{(1,31)} = 3.94$, $p = 0.06$, $\eta^2 = 0.11$.

EEG data acquisition and preprocessing

EEG data acquisition

The first EEG dataset was acquired simultaneously with the MEG data using a 70-channel MEG-compatible scalp electrode system (BrainProducts, München). Signals were digitized at 1000Hz, with an online bandpass filter of 0.03 - 300Hz. The second EEG dataset was recorded using a Biosemi Active-Two acquisition system from 32 active electrodes in a modified 10/20 system montage. Signals were digitized at 512Hz, with a bandpass of DC - 104Hz, and EEG channels were referenced offline to the average of the left and right mastoid channels. Impedances were kept at < 30kΩ at all scalp sites for both studies.

EEG data preprocessing

Both EEG datasets were preprocessed using the Fieldtrip software package, an open-source Matlab toolbox (Oostenveld et al., 2011). For RSA, we planned to combine the two EEG datasets to maximize power. Therefore, given that the two datasets were acquired with different online filtering settings (0.03 - 300Hz vs. DC - 104Hz), we applied an offline low-pass filter of 30Hz to the first EEG dataset, and an offline band-pass filter of 0.1 - 30Hz to the second EEG dataset. In addition, because the two datasets were acquired with different sampling rates (1000Hz vs. 512Hz), we down-sampled both datasets to 500Hz.

Just as for the MEG data, each individual's EEG data was segmented into epochs. We identified and removed on average seven bad EEG channels out of the 70 channels in the first EEG dataset, whereas no bad channels were identified or removed in the second EEG dataset. We applied an Independent Component Analysis (ICA; Bell and Sejnowski, 1997; Jung et al., 2000) and removed components associated with eye movement from the EEG signal. We then inspected the data visually and removed any remaining artifacts. The data of the 7 bad EEG channels in the first dataset were then interpolated using spherical spline interpolation (Perrin et al., 1989).

On average, slightly more artifact-free trials remained following the *animate constraining* (81 trials on average) than the *inanimate constraining* verbs (79 trials on average), $F_{(1,71)} = 9.12$, $p = 0.004$, $\eta^2 = 0.114$.

RSA for both MEG and EEG data

We used the same method of carrying out the RSA for the MEG and the EEG data, using MATLAB 2014b (MathWorks) with custom-written scripts. For the EEG RSA, we combined the two EEG datasets (72 individuals in total) in order to increase the statistical power (we subsequently tested whether the two EEG datasets showed a statistically significant difference for the reported effect, see Results).

A schematic illustration of our RSA approach is shown in Figure 2. First, in each participant, for each trial, and at each time point, we extracted a vector of data that represented the *spatial pattern of neural activity* across all sites (MEG: 306 sensors; first EEG dataset: 70 electrodes; second EEG dataset: 32 electrodes). At each time point, *t*, we quantified the similarity between the spatial pattern of neural activity following all possible pairs of *animate constraining* verbs (e.g. between A-S1 and A-S2, between A-S1 and A-Sn, in Figure 2) and all possible pairs of *inanimate constraining* verbs (e.g. between B-S1 and B-S2, between B-S1 and B-Sn in Figure 2) by calculating a *Pearson's r* value between the spatial vectors. These pairwise correlation R-values were used to construct spatial similarity matrices at each time point, corresponding to the spatial similarity patterns of neural activity following the *animate constraining* verbs (the left matrix in Figure 2) and the *inanimate constraining* verbs (the right matrix in Figure 2). We then averaged the N*(N-1)/2 off-diagonal elements of these matrices to compute an averaged R-value at each time point that corresponded to the average spatial similarity pattern following *animate constraining* and *inanimate constraining* verbs. We plotted these average values at each consecutive time point to yield two time-series of spatial similarity R-values in each participant, reflecting the temporal dynamics of the spatial similarity of brain activity produced following the *animate constraining* verbs (the solid red line in Figure 2) and the *inanimate constraining* verbs (the dotted blue line in Figure 2).

Insert Figure 2 here

Statistical analysis: cluster-based permutation test

We then asked whether and when there were significant differences in the spatial similarity pattern of neural activity following the *animate constraining* and the *inanimate constraining* verbs, using cluster-based permutation tests to control for multiple comparisons across multiple time points (Maris and Oostenveld, 2007). Specifically, at each time point from the onset of the verb (t = 0) until before the direct object noun actually appeared (t = 1100ms), we carried out a paired t-test (550 tests in total). Adjacent data points that exceeded a pre-set uncorrected p-value threshold of 0.05 were considered temporal clusters. The individual t-statistics within each cluster were summed to yield a cluster-level test statistic — the cluster mass statistic. We then randomly re-assigned the spatial similarity R-values across the two conditions (i.e. *animate constraining* and *inanimate constraining* verbs) at each time point within each participant, and calculated cluster-level statistics as described above. This was repeated 10000 times. For each randomization, we took the largest cluster mass statistic (i.e. the summed t values), and, in this way, built a null distribution for the cluster mass statistic. We then compared our observed cluster-level test statistic against this null distribution. Any temporal clusters falling within the highest or lowest 2.5% of the distribution were considered significant.

Results

RSA results

For both the MEG and the EEG datasets, we quantified the spatial similarity pattern of neural activity produced following the *animate constraining* and the *inanimate constraining* verbs at each time point during the predictive time window (from the onset of the verb until before the direct object noun actually appeared). As shown in Figure 2, these spatial similarity values were computed by correlating the spatial pattern of activity (across all sensors/channels) between all possible pairs of items within each condition, and then averaging these values to yield two time series in each participant — one that corresponded to activity produced following the *animate constraining* verbs and the other that corresponded to activity produced following the *inanimate constraining* verbs.

MEG results

Figure 3A, left, shows the group-averaged (32 participants) MEG time series of spatial similarity values following the *animate constraining* and the *inanimate constraining* verbs. This reveals a sharp increase in the overall degree of spatial similarity beginning at ~50ms after verb onset, peaking twice between 100 and 200ms, decreasing with a third, relatively broader peak between 300 - 400ms following verb onset. After then, the spatial similarity values decrease throughout the duration of the verb. These three peaks may reflect the strong evoked activity produced by the bottom-up input of the verb (corresponding to the N1, P2 and N400 components). A similar, rapid increase in the spatial similarity pattern was observed following the onset of the determiner, which immediately followed the verb at 550ms, peaking at ~150ms and ~225ms following determiner onset before gradually decreasing again (again likely reflecting the N1 and P2 components evoked by the determiner; there was no third peak, consistent with the lack of a strong evoked N400 following the determiner).

Of most relevance to the questions addressed in this study, from around the time of verb *offset* (450ms after verb onset), the spatial similarity patterns appeared to diverge such that the spatial pattern of neural activity was more similar following the *animate constraining* than the *inanimate constraining* verbs. This difference continued into interstimulus interval (100ms), disappearing at ~50ms following the onset of the determiner (i.e. lasting from ~450 to ~600ms after verb onset). A mass univariate analysis at all time points across the entire epoch (0 - 1100ms) using cluster-based permutation methods to account for multiple comparisons (Maris and Oostenveld, 2007) confirmed a significant difference in spatial similarity ($p = 0.0073$), with a cluster between 529 - 599ms following verb onset (although note that this is likely to underestimate of the true extent of the effect, see Maris and Oostenveld, 2007). Figure 3A, right, shows a scatter plot of the averaged R-values per participant across the 500 - 600ms time window following verb onset. This shows that 26 out of the 32 participants had R-values above the diagonal line, i.e. larger spatial similarity values following the *animate constraining* than the *inanimate constraining* verbs. Given that, if anything, the semantic similarity structure of the *animate constraining* verbs was slightly *lower* than that of the *inanimate constraining* verbs, and that these two groups of verbs were matched on their lexical similarity structures (including length, orthographic neighborhood and log frequency, see Materials and Methods), we attribute this spatial similarity effect (e.g. *animate constraining* > *inanimate constraining*) to the *prediction* of *animate* versus *inanimate* semantic features of the upcoming nouns.

Insert Figure 3 here

We then asked whether this spatial similarity effect was modulated by overall discourse constraint — that is, whether it depended on being able to predict a specific upcoming lexical item. In minimal contexts, all verbs had relatively low lexical constraints (< 24%, as verified by our first cloze norming study). However, by design, and as verified by our second cloze norming study, 50% of the *animate constraining* and 50% of the *inanimate constraining* verbs appeared in discourse contexts that, in conjunction with the verb, constrained strongly for a specific upcoming noun (*high discourse constraint*; mean constraint: 68% +/- 15%), while 50% of the *animate constraining* and 50% of the *inanimate constraining* verbs appeared in discourse contexts that did not constrain strongly for a specific noun (*low discourse constrain*t; mean constraint: 22% +/- 12%). As shown in Figure 3B, the spatial similarity effect appeared to be equally large following the *high discourse constraint* contexts (Figure 3B: left) and the *low discourse constraint* contexts (Figure 3B: right). To statistically quantify this, we averaged the spatial similarity values between 500 - 600ms relative to verb onset (when the effect was maximal) separately for each of the four conditions and used these values as the dependent measure in a repeated measures ANOVA in which Verb animacy constraint (*animate constraining*, *inanimate constrainin*g) and Discourse constraint (*high discourse constraint*, *low discourse constraint*) served as within-subjects factors. This analysis confirmed the main effect of Verb animacy constraint ($F_{(1,31)}$ = 12.05, p = 0.002, η2 = 0.28), but failed to reveal either an interaction between Verb animacy constraint and Discourse constraint ($F_{(1,31)}$ = 0.20, p = 0.66, η2

= 0.01), or a main effect of Discourse constraint ($F_{(1,31)}$ = 2.43, p = 0.13, η2 = 0.07).

EEG results

Figure 4A (left) presents the group-averaged (combined across the two EEG datasets: 72 participants in total) EEG time series of spatial similarity values following *animate constraining* and *inanimate constraining* verbs. Similar to MEG, the overall spatial similarity appeared to increase rapidly from ~50ms after verb onset, with two sharp peaks at 100ms and 200ms post verb onset, and then a relatively lower and broader peak between 300 - 400ms following verb onset. Following the onset of the determiner, we observed a similar rapid increase, with three sharp peaks at ~50ms, ~175ms and 200ms post determiner onset, but no obvious peak between 300 - 400ms.

Again, of most theoretical interest was whether the spatial similarity pattern of neural activity differed following the *animate constraining* versus the *inanimate constraining* verbs. As shown in Figure 4A (left), similar to MEG, there did indeed appear to be a difference, with larger spatial similarity values following the *animate constraining* than following the *inanimate constraining* verbs from ~400ms after verb onset. This effect again continued into the interstimulus interval, lasting until around 100ms after determiner onset. A mass univariate analysis at all time points across the entire epoch (from 0 to 1100ms relative to the onset of verbs), using cluster-based permutation methods to account for multiple comparisons (Maris and Oostenveld, 2007), confirmed this difference, revealing two significant clusters between 420 - 512ms, p = 0.024, and between 530 - 636ms, p = 0.0003 relative to the verb onset (again, likely to underestimate the true extent of the effect, see Maris and Oostenveld, 2007). Figure 4A (right) shows a scatter plot of the averaged R-values per participant within the 450 - 650ms time window. Two thirds of participants had R-values above the diagonal line, indicating that the majority of participants showed greater spatial similarity values following the *animate constraining* than the *inanimate constraining* verbs.

Insert Figure 4 here

Just as for the MEG dataset, we also asked whether the spatial similarity effect was modulated by the lexical constraint of the broader discourse context. We calculated the spatial similarity time series separately for the *animate constraining* and *inanimate constraining* verbs in the *high discourse constraint* and *low discourse constraint* contexts (see Figure 4B), and, for each condition, averaged the spatial similarity values between 450-650ms (where the spatial similarity effect was maximal), and entered the averaged values into a repeated-measures ANOVA, as described above for the MEG dataset. Again, while this analysis confirmed the main effect of Verb animacy constraint ($F_{(1,71)} = 23.65$, $p < 0.001$, $\eta^2 = 0.25$), there was no interaction between Verb animacy constraint and Discourse constraint ($F_{(1,71)} = 0.42$, $p = 0.52$, $\eta^2 = 0.01$), and no main effect of Discourse constraint ($F_{(1,71)} = 0.22$, $p = 0.64$, $\eta^2 = 0.003$).

Finally, we asked whether the observed spatial similarity effect differed between the two EEG datasets by carrying out an additional ANOVA with spatial similarity values averaged between 450 - 650ms as the dependent measure. In this analysis, Dataset (dataset 1, dataset 2) was a between-subject factor, while Verb animacy constraint (*animate constraining*, *inanimate constraining*) and Discourse constraint (*high discourse constraint, low discourse constraint*) were within-subjects factors. This analysis revealed a significant main effect of Verb animacy constraint ($F_{(1,70)} = 22.28$, $p < 0.001$, $\eta 2 = 0.24$) as well as a significant interaction between Dataset and Verb animacy constraint ($F_{(1,70)} = 5.15$, $p = 0.026$, $\eta^2 = 0.07$). Follow-up analyses in each dataset separately showed a near-significant main effect of Verb animacy constraint in the first dataset, $F_{(1,31)} = 3.58$, $p = 0.068$, $\eta^2 = 0.10$, and a more robust main effect of Verb animacy in the second dataset, $F_{(1,39)} = 22.99$, $p < 0.001$, $\eta^2 = 0.37$. No other interactions were found.

Summary

In sum, the MEG and EEG findings were quite consistent. This type of convergence is consistent with a recent study, also using EEG and MEG together with RSA, which decoded visual representations of living versus non-living objects (Cichy and Pantazis, 2017). In particular, we note that the smaller number of recording sites used to collect the EEG data (70 electrode sites in the first study and 32 electrode sites in the second study) in comparison with the MEG data (306 MEG channels) did not appear to sacrifice our ability to detect a robust spatial similarity effect using EEG, again similar to the previous study (see Cichy and Pantazis, 2017, supplementary materials).

Behavioral findings

We did not acquire behavioral data on the verb itself. However, in both experiments, at the end of each scenario, participants made acceptability judgments, with acceptability determined by whether the direct object noun matched or violated the animacy constraints of the verb. In the MEG-EEG experiment, participants made correct judgments in 84.09% of scenarios on average (SD: 7.32%), with no differences between scenarios that contained *animate constraining* and *inanimate constraining* verbs ($t_{(31)} = 1.60$, $p = 0.12$). In the EEG-only study, participants made correct judgments in 89.17% of scenarios on average (SD: 5.26%), again with no differences between scenarios containing *animate constraining* and *inanimate constraining* verbs ($t_{(31)} = 0.71$, $p = 0.48$).

In addition to making acceptability judgments after each scenario, participants also responded to Yes/No questions that followed a subset of scenarios. In the MEG-EEG study, on average, 76.56% of the 24 comprehension questions were answered correctly (SD: 16.18%), and in the EEG-only study, 84.94% of the 32 comprehension questions were answered correctly (SD: 6.75%). These findings indicate that participants attended to the context information within the discourse scenarios, rather than only the final sentences.

Discussion

We used spatial RSA, in combination with MEG and EEG to ask whether comprehenders use verb constraints to predict the animacy of upcoming nouns. Our findings were robust and strikingly convergent across the MEG (n=32) and EEG (n=72) datasets (see also Cichy and Pantazis, 2017). The spatial pattern of neural activity following *animate constraining* verbs was significantly more similar than following *inanimate constraining* verbs. This effect began at approximately 450ms (EEG)/500ms (MEG) after verb offset, and it ended well before the presentation of the noun. Moreover, it was just as large following non-constraining discourse contexts as following discourse contexts that constrained strongly for a specific upcoming noun.

The spatial pattern of brain activity was more similar following *animate constraining* than *inanimate constraining* verbs

We take the increased spatial similarity of neural activity following *animate constraining* versus *inanimate constraining* verbs as evidence that comprehenders *predicted* the animacy of the upcoming noun. Before discussing this interpretation in more detail, we first consider alternative explanations.

One possibility is that, instead of reflecting anticipatory activity related to the upcoming noun, the spatial similarity effect was driven by differences in the semantic and/or lexical similarity structures of the verbs themselves. Of course, a verb's constraints for its upcoming arguments are *part* of its lexical structure (McCawley, 1968; Jackendoff, 1993), and the goal of this study was to determine *when* these constraints became available during online comprehension. However, there are many other aspects of a verb's meaning and form that are unrelated to its arguments, and it is possible that, in our materials, these other features of the verbs covaried with their animacy constraints. For example, the two *animate constraining* verbs, "cautioned" and "alarmed", are more similar to each other than the two *inanimate constraining* verbs, "folded" and "distributed", not *only* because they both constrain for upcoming animacy features, but *also* because both their meanings are specific instances of the broad meaning defined by "warn", and are equally frequent, and because both words have similar lengths.

These types of differences, however, are unlikely to explain the present set of findings. First, semantic similarity measures (Wu and Palmer, 1994) did not show a greater similarity among *animate constraining* than *inanimate constraining* verbs (if anything, there was a small effect in the other direction); there were also no differences between the two groups of verbs in their similarity structures based on various lexical variables. Second, the spatial similarity effect occurred relatively late, starting to emerge at around 450ms (EEG)/500ms (MEG) following verb onset, which is past the stage at which lexical and semantic factors would be expected to modulate brain activity (Grainger and Holcomb, 2009).

Another possible explanation for our findings is that, instead of reflecting anticipated differences in the *semantic* similarity structure of the upcoming nouns, they reflected predicted differences in their syntactic or lexical similarity structures. This again seems unlikely. While verbs that constrain for *animate* nouns tend to constrain for fewer types of thematic/syntactic structures than verbs that constrain for *inanimate* nouns (Kipper et al., 2006), the verbs in the current study had a transitive bias, and they appeared in the same subject-verb-noun syntactic structure throughout the experiment. Therefore, comprehenders are likely to have predicted an upcoming direct object, regardless of the verb's animacy constraint. In addition, we verified that similarities based on lexical factors (word length, orthographic neighborhood and log frequency) were matched between the subset of predicted *animate* and *inanimate* nouns that followed the subset of high constraint discourse contexts.

Having considered these alternative explanations, we now turn to our preferred interpretation — that the difference in the spatial similarity pattern following the *animate constraining* and the *inanimate constraining* verbs reflected differences in the similarity structure of *predicted* semantic features that were linked to the animacy of the anticipated upcoming nouns. As noted in the Introduction, semantic features that characterize animate nouns are more strongly intercorrelated than those that characterize inanimate nouns (McRae et al., 1997; Devlin et al., 1998; Garrard et al., 2001; Randall et al., 2004; Zannino et al., 2006), and we verified that this was true of the likely anticipated nouns in the present study. Because the neural representations of semantic features are widely distributed across the cortex (Martin and Chao, 2001; Thompson-Schill, 2003), such differences in semantic similarity structure will produce differences in spatial similarity patterns of neural activity. In previous studies, these differences are likely to have contributed to the ability of RSA to successfully decode animacy from bottom-up linguistic (Sudre et al., 2012; Bruffaerts et al., 2013; Devereux et al., 2013) and non-linguistic (Kriegeskorte et al., 2008b; Carlson et al., 2013; Cichy et al., 2014; Proklova et al., 2016; Cichy and Pantazis, 2017) inputs. In the present study, we suggest that the divergence in similarity patterns following the *animate constraining* and *inanimate constraining* verbs resulted from the *prediction* of animacy features *before* new bottom-up inputs become available.

The prediction of upcoming animacy features was not dependent on the prediction of a specific word

While previous studies of anticipatory neural processing during language comprehension have reported effects associated with the prediction of specific upcoming words (e.g. Wicha et al., 2004; DeLong et al., 2005; Van Berkum et al., 2005; but see Nieuwland et al., 2018), the present findings provide neural evidence for the prediction of semantic features that characterize whole sets of words. We further showed that predicting these broad sets of semantic features did not depend on being able to predict a single word: the spatial similarly effect was just as large following low constraint as following high constraint discourse contexts.

This finding has important implications. It has sometimes been argued that, because most words are not highly predictable on the basis of their prior contexts, predictive processing is unlikely to play a major role in language comprehension. Implicit in this argument is the assumption that we are only able to predict upcoming lexical items. We and others, however, have argued that comprehenders are able to predict upcoming information, with various degrees of certainty, at multiple levels and grains of representation (e.g. Altmann and Mirković, 2009; Kuperberg and Jaeger, 2016). The present findings show that, despite not being able to predict upcoming words, the constrains of the verb provided enough information for comprehenders to predict upcoming semantic features that distinguished between upcoming *animate* and *inanimate* items.

The time course of the prediction effect

As noted above, the spatial similarity effect began past the stage at which comprehenders are likely to have accessed other lexico-semantic features of the verb, and well before the argument actually appeared. We suggest that this was the first time point at which comprehenders were able to infer the full high-level event structure (e.g. <Agent cautioned animate noun>), and that they used this structure to generate top-down predictions of the semantic features linked to the animacy of upcoming arguments (see Altmann and Mirković, 2009; Kuperberg and Jaeger, 2016; Kuperberg et al., 2019).

Despite its early onset, the spatial similarity effect lasted for only around 150ms (MEG)/200ms (EEG). This is consistent with a recent MEG-RSA study in which we used a different paradigm in a different language (Chinese) to capture the prediction of specific individual words (Wang et al., 2018). These types of short-lived prediction effects might seem surprising if one assumes that pre-activated mental representations are necessarily accompanied by persistent and sustained detectable neural activity. However, evidence from intracranial recordings of local neural activity (Mongillo et al., 2008; Stokes et al., 2013; Lundqvist et al., 2016; Bastos et al., 2018; Lundqvist et al., 2018b), and from noninvasive EEG and fMRI recordings of global brain activity (Sprague et al., 2016; Wolff et al., 2017), suggests that, instead of being persistent, neural activity over delays is, in fact, relatively sparse. During these delays, anticipated information remains accessible, but it can only be *detected* when perturbed or "pinged", e.g. by a targeted pulse of transcranial magnetic stimulation (Rose et al., 2016), or by new bottom-up input (Wolff et al., 2017). This has led to the hypothesis that anticipated information is held in an "activity silent" state (Stokes, 2015; Lundqvist et al., 2018a), becoming available only when it is task relevant (Sprague et al., 2016; Lundqvist et al., 2018b). Extrapolating to the present findings, we speculate that, despite the absence of a spatial similarity effect immediately preceding the noun, the predicted animacy-based semantic features were nonetheless available to facilitate semantic processing of the incoming noun when it appeared. As in many previous studies (e.g. Paczynski and Kuperberg, 2011, 2012; Szewczyk and Schriefers, 2011), this facilitation manifested on the N400 ERP component, which was smaller to nouns that matched versus mismatched these predicted animacy features (see Kuperberg et al., 2019, for a full report of ERP effects after noun onset). In future work, it will also be important to determine whether similar dynamics are observed when bottom-up input unfolds at a more naturalistic rate during spoken language comprehension.

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Figure legends

Figure 1. Pairwise Wu & Palmer similarity values for the senses of (A) *animate constraining* and *inanimate constraining* verbs and (B) nouns that confirmed these animacy constraints. The range of these Wu & Palmer similarity values is between 0 and 1, with values approaching 0 indicating low similarity, and a value of 1 indicating identical concepts. (A) Pairwise Wu-Palmer semantic similarity values of the verbs are shown in a 250 by 250 symmetric semantic similarity matrix, with rows and columns indexing the individual verbs' senses (*animate constraining* verbs: from 1 to 113; *inanimate constraining* verbs: from 114 to 250). The pairwise Wu-Palmer semantic similarity values of the *animate constraining* verbs (values at the top-left of the matrix) were smaller than those of the *inanimate constraining* verbs (values at the bottom-right of the matrix): p = 0.04 (1000 permutations). (B) Pairwise Wu-Palmer semantic similarity values of the nouns are shown in a 244 by 244 symmetric semantic similarity matrix, with rows and columns indexing the individual nouns' senses (animate nouns: from 1 to 116; inanimate nouns: from 117 to 244). The pairwise Wu-Palmer semantic similarity values of the *animate nouns* (values at the top-left of the matrix) were larger than those of the *inanimate nouns* (values at the bottom-right of the matrix): p = 0.001 (1000 permutations).

Figure 2. A schematic illustration of the spatial Representational Similarity Analysis in the present study. First, in each participant, for each trial, and at each time point, *t*, a vector of data was extracted across all MEG/EEG sites to represent the spatial pattern of neural activity produced at that time point. Second, at each time point, *t*, the similarity between the spatial pattern of neural activity produced by all possible pairs of trials of condition A (e.g. between

A-S1 and A-S2, between A-S1 and A-Sn within the left side of the box) and all possible pairs of trials of condition B (e.g. between B-S1 and B-S2, between B-S1 and B-Sn within the right side of the box) was quantified by calculating the *Pearson's r* values between the spatial vectors. These pairwise correlation R-values were used to construct spatial similarity matrices at each time point, corresponding to the spatial similarity patterns of neural activity produced in condition A (the left matrix) and condition B (the right matrix). Third, the N*(N-1)/2 off-diagonal elements of these matrices were averaged to compute an averaged R-value at each time point that corresponded to the average spatial similarity pattern produced by each of the two conditions. These average values at each consecutive time point yielded two time-series of spatial similarity R-values in each participant, reflecting the temporal dynamics of the spatial similarity of brain activity produced in conditions A (red solid line) and condition B (blue dotted line).

Figure 3. Results of spatial similarity analysis of the MEG data (study 1, 32 participants). (A) Left: Group-averaged time series of spatial similarity values following *animate constraining* verbs (red solid line) and following *inanimate constraining* verbs (blue dotted line), from verb onset at 0ms to noun onset at 1100ms. The duration of the verbs (0 - 450ms) and the subsequent determiners (550 - 1000ms) are marked with grey bars on the x-axis. The spatial pattern of neural activity was more similar following the *animate constraining* than the *inanimate constraining* verbs between 529 - 599ms following verb onset (p = 0.0073, 10000 permutations); the significant cluster is highlighted by a black line over the time series. Right: A scatter plot of the averaged R-values per participant across the 500 - 600ms time window following verb onset. This shows that 26 out of the 32 participants had R-values above the diagonal line, i.e. larger spatial similarity values following the *animate constraining* than the *inanimate constraining* verbs. (B) Group-averaged time series of the spatial similarity values following the *animate constraining* (red solid line) verbs and following the *inanimate constraining* verbs (blue dotted line) in the *high discourse constraint* scenarios that constrained strongly for a specific upcoming noun (left) and the *low discourse constraint* scenarios that did not constrain strongly for a specific noun (right). The spatial similarity effect was equally large following the two types of *discourse constraint* contexts, as indicated by the absence of an interaction between Verb animacy constraint and Discourse constraint ($F_{(1,31)} = 0.20$, p = 0.66, $\eta_2 = 0.01$), for the averaged spatial similarity values between 500 - 600ms following verb onset.

Figure 4. Results of spatial similarity analysis of the EEG data (combined across the two EEG datasets, 72 participants). (A) Left: Group-averaged time series of spatial similarity values following *animate constraining* verbs (red solid line) and following *inanimate constraining* verbs (blue dotted line), from verb onset at 0ms to noun onset at 1100ms. The duration of the verbs (0 - 450ms) and the subsequent determiners (550 - 1000ms) are marked with grey bars on the x-axis. The spatial pattern of neural activity was more similar following the *animate constraining* than the *inanimate constraining* verbs between 420 - 512ms (p = 0.024) and between 530 - 636ms (p = 0.0003) following verb onset (10000 times permutations); the significant cluster is highlighted by a black line over the time series. Right: A scatter plot of the averaged R-values per participant across the 500 - 600ms time window following verb onset. This shows that two thirds of participants had R-values above the diagonal line, i.e. larger spatial similarity values following the *animate constraining* than the *inanimate constraining* verbs. (B) Group-averaged time series of spatial similarity values following *animate constraining* (red solid

line) and *inanimate constraining* (blue dotted line) in the *high discourse constraint* scenarios that constrained strongly for a specific word (left) and the *low discourse constraint* scenarios that did not constrain strongly for a specific noun (right). The spatial similarity effect was equally large following the two types of *discourse constraint* contexts, as indicated by the absence of an interaction between Verb animacy constraint and Discourse constraint ($F_{(1,71)} = 0.42$, $p = 0.52$, $\eta_2 = 0.01$) for the averaged spatial similarity values between 450 - 650ms following verb onset.

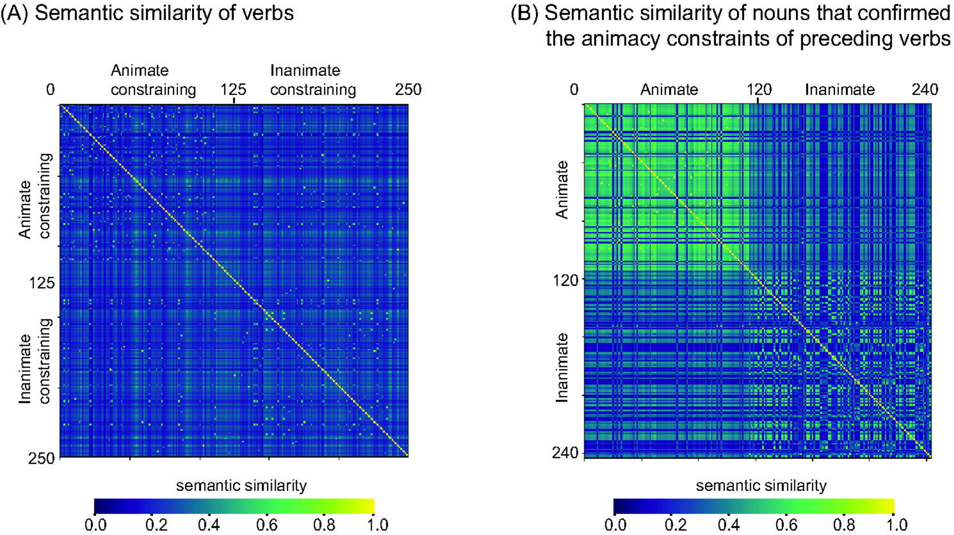
Table

Table 1. Examples of the four experimental conditions.

Verb animacy constraint	Discourse constraint	Example	*Lexical constraint of discourse context
Animate constraining	High discourse constraint	The lifeguards received a report of sharks right near the beach. Their immediate concern was to prevent any incidents in the sea. Hence, they cautioned the ...	65% (15%)
	Low discourse constraint	Eric and Grant received the news late in the day. They mulled over the information, and decided it was better to act sooner rather than later. Hence, they cautioned the ...	19% (11%)
Inanimate constraining	High discourse constraint	Judith was working on the origami project for her office fundraiser. She was starting to get frustrated because it was her third attempt at making a crane. Nevertheless, she unfolded the …	71% (14%)
	Low discourse constraint	Judith was nearing the end of her rope. She didn't think she could keep going. Nevertheless, she unfolded the …	24% (13%)

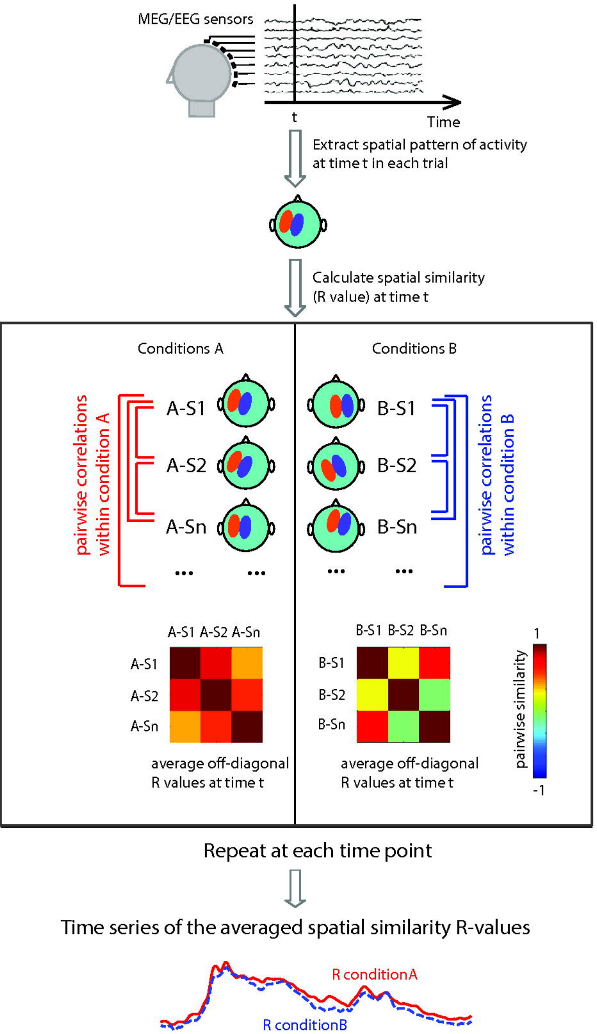
Note: Discourse scenarios were created around *animate constraining* and *inanimate constraining* verbs ("cautioned" and "unfolded"; underlined here but not in the experiment itself). The sentences continued with object nouns plus three additional words, as indicated by the three dots.

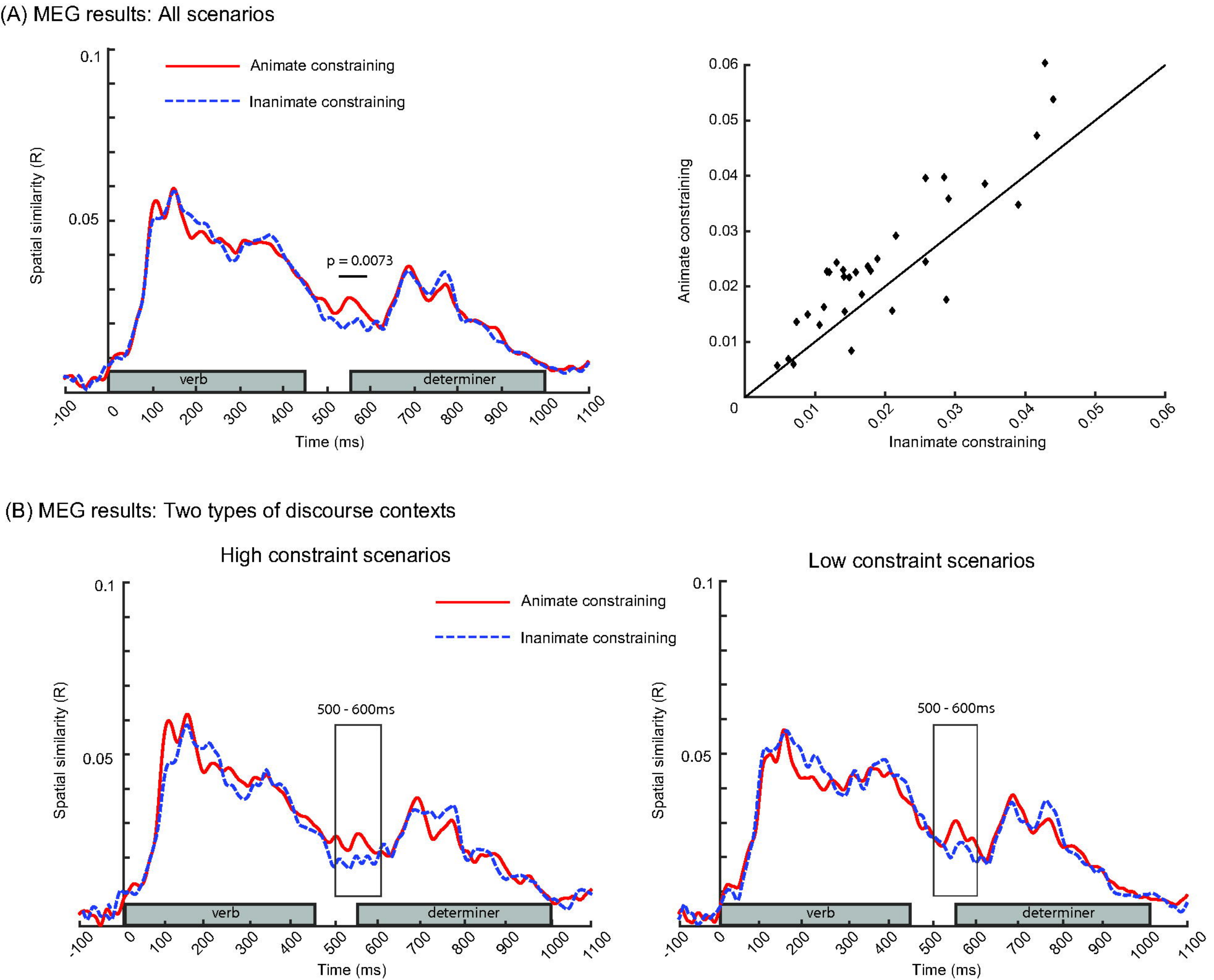
*The lexical constraint of the discourse context was operationalized as the percentage of participants who produced the best completion in a cloze study (see main text). Mean values are shown with standard deviations in parentheses.



(A) Semantic similarity of verbs

(B) Semantic similarity of nouns that confirmed the animacy constraints of preceding verbs


MEG/EEG sensors
t
Time
Extract spatial pattern of activity at time t in each trial
Calculate spatial similarity (R value) at time t
Conditions A
Conditions B
pairwise correlations within condition A
A-S1
A-S2
A-Sn
...
B-S1
B-S2
B-Sn
pairwise correlations within condition B
A-S1 A-S2 A-Sn
B-S1 B-S2 B-Sn
1
pairwise similarity
-1
average off-diagonal R values at time t
average off-diagonal R values at time t
Repeat at each time point
Time series of the averaged spatial similarity R-values
R conditionA
R conditionB

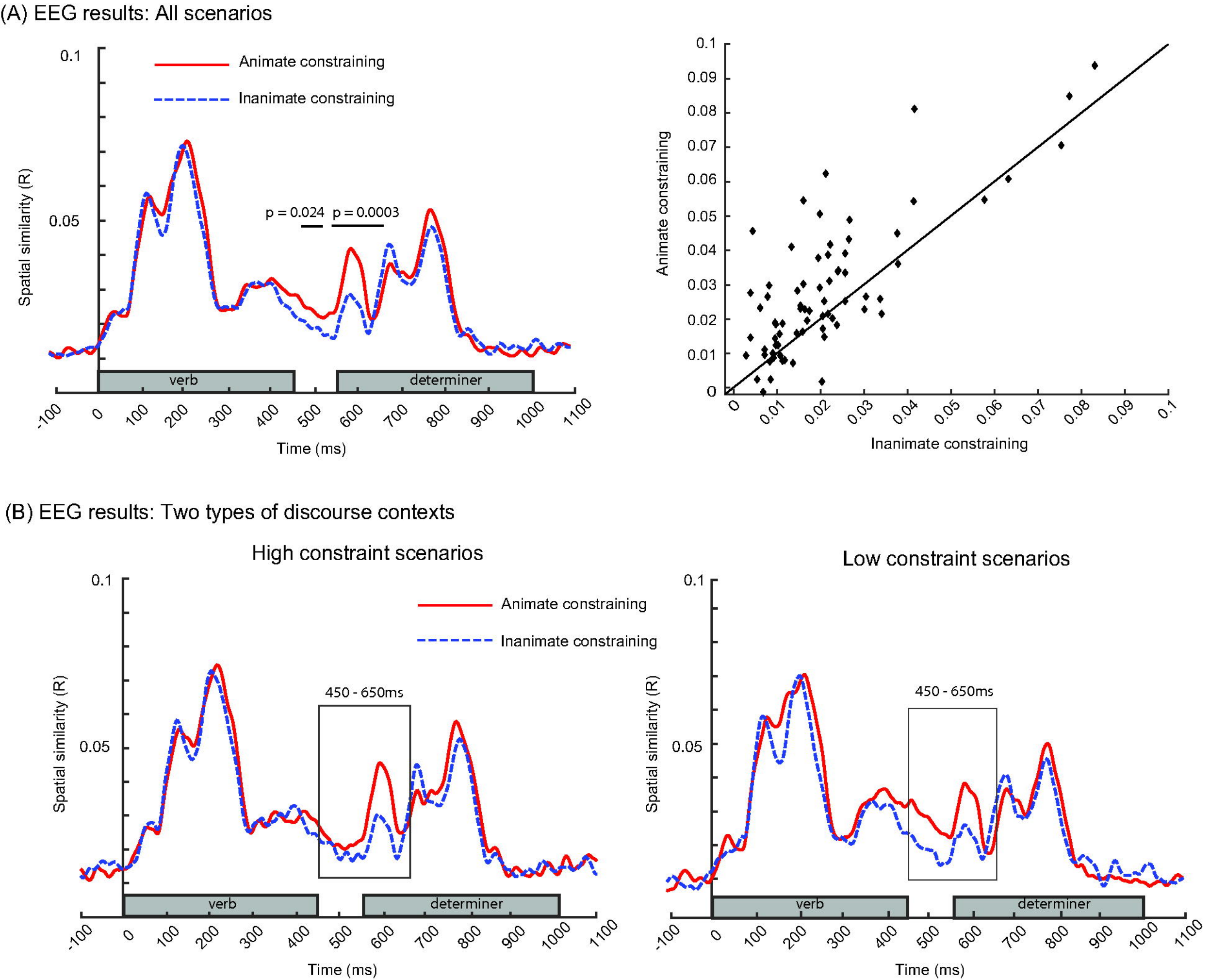


(A) MEG results: All scenarios

(B) MEG results: Two types of discourse contexts

High constraint scenarios

Low constraint scenarios



(A) EEG results: All scenarios

(B) EEG results: Two types of discourse contexts