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Playing "Duck Duck Goose" With Neurons: Change Detection Through Connectivity Reduction

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Abstract

Reduced connectivity between sending and receiving neurons (i.e., *synaptic depression*) may facilitate change detection by reducing responses for recently viewed objects so new objects can be highlighted. In the experiment reported here, we investigated high-level change detection following *semantic satiation*, which is the loss of meaning following repetition of a word. A computer simulation of a word-reading neural network with synaptic depression identified key predictions of connectivity reduction. A dynamic-causal-modeling analysis of magnetoencephalography (MEG) responses collected during a category-matching task identified connectivity reduction between a cortical region related to orthography and a cortical region related to semantics as the cause of the reduced MEG response to a repeated word. As predicted, prior repetitions of a category-matching word presented immediately after the repeated word enhanced semantic novelty, as measured with the M400 component. These results demonstrate that a combination of neural-network modeling and connectivity analyses can reveal the manner in which connectivity fluctuations underlie cognitive functions.

Keywords

semantic satiation, magnetoencephalography (MEG), M400, N400, dynamic causal modeling (DCM), synaptic depression, repetition suppression, cognitive neuroscience, neuroimaging, reading, cognitive processes

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Like many visual animals, humans rapidly detect the abrupt appearance of new objects if there are no distractions (O'Regan, Rensink, & Clark, 1999). This necessitates a constant comparison between the current input and the previous input. This comparison can be achieved by reducing the response to prior perceptions to make salient the appearance of anything new. But how is this critical mental function realized in the brain? In the study reported here, we tested the idea that connectivity reduction between sending and receiving neurons enhances change detection with minimal disruption (Francis, Grossberg, & Mingolla, 1994). Recent behavioral evidence shows that response reduction exists even for high-level concepts, such as a reduced desire to eat a particular food following repeatedly imagining eating that food (Morewedge, Huh, & Vosgerau, 2010). If connectivity reduction is a general mechanism for change detection, it should underlie not only perceptual reduction but also conceptual reduction. To test this claim, we examined electrophysiological responses while people performed a task designed to induce conceptual reduction in response to the repeated presentation of a word.

By drawing an analogy with the child's game of tin-can telephone (Fig. 1a), we can illustrate how connectivity reduction enhances change detection with minimal disruption to the communication network. In this game, two cans are connected by a string; when a person talks into one of the cans, another person can hear what the first person is saying by holding the other can to his or her ear. Suppose you are listening with a can to each ear and have a different friend on each line. If one friend

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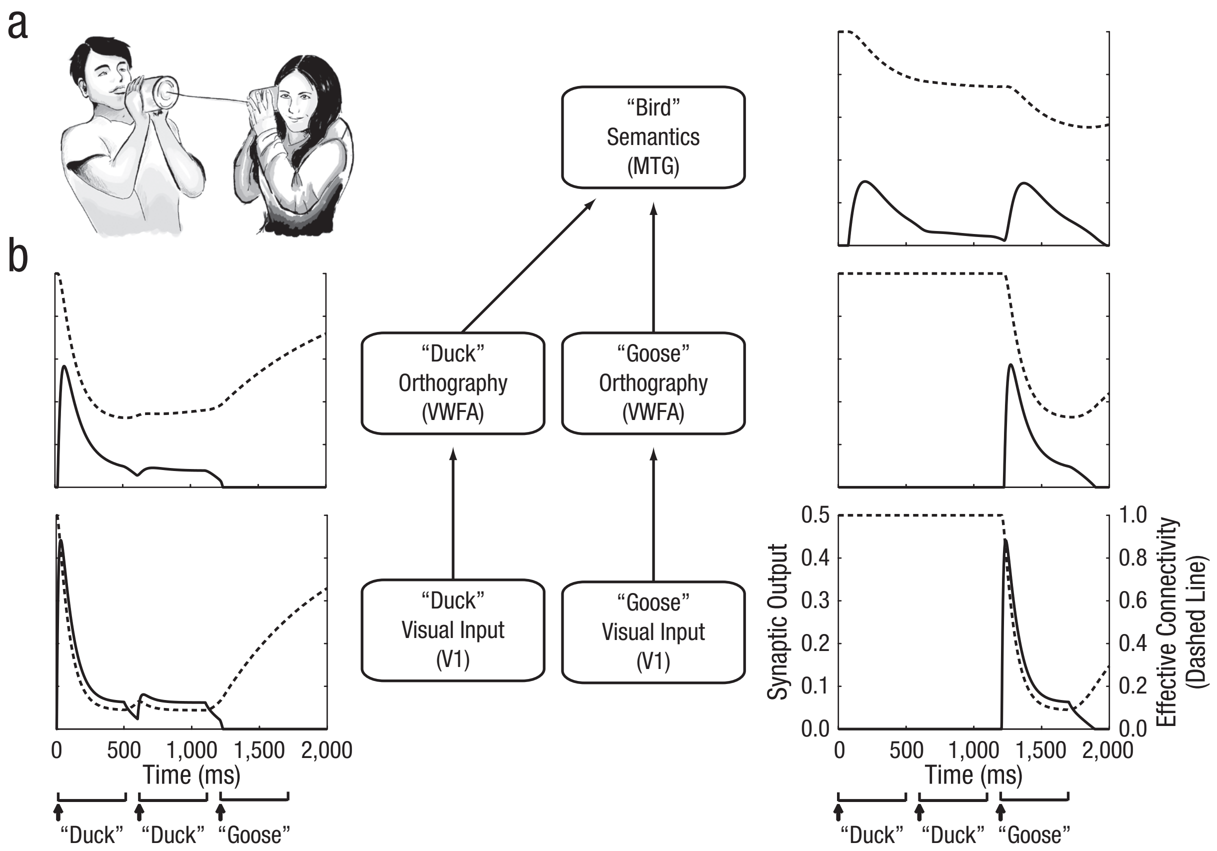

Fig. 1. An illustration of connectivity reduction. Similar to cutting the string connecting two cans in the child's game of tin-can telephone (a), a computer simulation of synaptic depression in an artificial neural network of reading (b) demonstrates that the semantic response to the word "duck" is reduced on repetition, but that it is recovered during presentation of the word "goose." In the illustration of the network, black arrows represent baseline connectivity. In the graphs, the dashed lines show effective connectivity as synaptic resources become depleted, and the solid lines show recent synaptic output. The graphs are shown adjacent to their corresponding synapses. Above-threshold membrane potential (e.g., firing rate) of sending neurons is not shown but is equivalent to the synaptic output divided by effective connectivity. V1 = primary visual cortex; VWFA = visual word-form area; MTG = middle temporal gyrus.

talks too loudly, you will not detect when the other friend begins to speak (i.e., a change of talker). This problem is solved if your loud friend loses the ability to speak (i.e., talker suppression). However, it may be that your loud friend has an important message that someone else needs to hear. A less disruptive solution is to weaken the string connecting you and your loud friend, which allows you to detect a change of talker while preserving the ability of your loud friend to talk to you. In this example, the talkers and listeners correspond to neurons, the strings correspond to synapses, and the solution of weakening the string corresponds to connectivity reduction.

A neural mechanism that implements connectivity reduction is *synaptic depression* (Grossberg, 1969; Tsodyks & Markram, 1997). Electrophysiology studies have found a temporary reduction of effective communication between sending and receiving neurons when the sender has been made to fire at a high rate (Thomson, 1997). This occurs because synaptic resources become depleted with recent activity—the sending neuron is talking loudly and the receiving neuron can still listen, but the message no longer gets through. Because the receiver is no longer driven at its maximal response, it is made sensitive to other input from other synapses (i.e., change detection becomes possible).

In previous work, we examined response reduction to visually presented stimuli by comparing responses to a word that was immediately repeated with responses to two unrelated words. A computer-simulation model of synaptic depression explained both the behavioral and electrophysiological data (Huber, Tian, Curran, O'Reilly, & Woroch, 2008). However, these experiments did not differentiate connectivity reduction from other forms of adaptation—for example, a model assuming suppression of the underlying representations might also explain the data. Here, we report a new simulation demonstrating a unique prediction of connectivity reduction. Using the previously published parameters, we examined a condition in which a word was repeated and then followed by a semantically similar word (e.g., "duck duck goose"). The model viewed each word for 500 ms with a 100-ms blank screen between each word (Fig. 1b). In the center of the figure, the bottom layer represents visual input, the middle layer represents orthography, and the top layer represents the semantic knowledge that ducks and geese are both birds.

As the figure shows, the semantic output to the second occurrence of "duck" was reduced owing to connectivity reduction. However, a subsequent presentation of "goose" replenished the semantic response because "goose" uses different synapses to activate the bird response. Through connectivity reduction, the model was made sensitive to the change between "duck" and "goose." As revealed by this simulation, the key to identifying connectivity reduction is the observation of a reduced response for repetitions combined with (a) the absence of a reduced response for sending neurons and (b) a demonstration that the receiving neurons are still capable of responding, which is revealed by their replenished response if a closely related object is presented. These last two elements rule out suppression of senders and receivers, thus isolating connectivity reduction as the underlying cause.

Our experimental paradigm concerned *semantic satiation* (Lambert & Jakobovits, 1960; Severance & Washburn, 1907), which is the loss of meaning for a repeated word. In a prior study, we assessed semantic satiation in three behavioral experiments (Tian & Huber, 2010). During each trial of a category-matching task, participants viewed a category name for 1 s before the appearance of a category member initiated a speeded match/mismatch decision. If prior repetitions of a category name induce semantic satiation through connectivity reduction, and if connectivity reduction enhances change detection, we predicted that people would become overly sensitive to the semantic change between words belonging to the same category (e.g., prior repetitions of "fruit" followed by "fruit-apple"); this should lead to reduced performance by giving the false impression that these words mismatched.

People performed blocks of 20 trials, with each block using the same category name for 10 trials (the repeated condition) and 10 different category names for the other 10 trials (the novel condition), with these conditions appearing in a random order. After the first trial for each condition, the nine additional occurrences of each condition were broken into thirds for the analyses. The repetition effect (measured as the response to repeated words minus the response to novel words) was calculated for each third. People were faster in the repeated category for the first third but, as predicted by connectivity reduction, they were slower for the final third.

An additional experiment failed to find slower responses if the category for each trial was indicated by a previously unseen category member (e.g., previous presentation of nine different words from the fruit category followed by "pear-apple"), and another experiment failed to find slower responses if the task was simple word matching rather than category matching (e.g., prior repetitions of "apple" followed by "apple-apple"). Respectively, these experiments ruled out suppression of semantic representations and suppression of orthographic representations, which supports the claim that semantic satiation is due to connectivity reduction between orthography and semantics. Paradoxically, this account assumes that heightened sensitivity to the small semantic differences between the repeated category name and a matching category memory produced the observed performance deficit. In the current study, we tested this explanation by measuring magnetoencephalography (MEG) responses, and the M400 in particular, to determine whether repeated presentation of the category name enhanced semantic novelty for a matching category member. In addition, we used dynamic causal modeling (DCM; David et al., 2006) to directly test whether this enhanced semantic novelty was due to reduced connectivity.

Method

Participants

Thirteen individuals received financial compensation for participating in the study. All participants were right-handed native-English speakers with no history of neurological disorder.

Materials

The category names and category members were the same as those used in Experiment 1b of our previous behavioral study (Tian & Huber, 2010). Sixteen single-word category names were selected, and 20 single-word category members were selected for each category (see Appendix 1b in Tian & Huber, 2010). All words were displayed in uppercase Times New Roman font, as yellow lettering against a black background, and subtended less than 3° of visual angle. Stimulus materials were projected on a screen inside a MEG chamber. Two 2-button response boxes were used, one for each hand. One button on each response box was assigned to a response.

Procedure

The speeded category-matching task used in Experiment 1b of our previous behavioral study (Tian & Huber, 2010) was replicated in this experiment. On each trial, a category name was presented above the midline for 1,000 ms, followed by a category member presented below the midline; both category name and category member remained on screen until participants responded. Participants were asked to decide as quickly and as accurately as possible whether the category member belonged to the named category. A blank screen was presented for 500 ms between trials to minimize artifacts caused by eye blinks.

A 2 (repetition status: repeated vs. novel) × 2 (match status: match vs. mismatch) factorial design was used, with five repetitions of the four conditions across the 20 trials in a block. The order of these 20 trials was determined randomly. One of the 16 category names was chosen to repeat on 10 trials (repeated condition), and 10 different category names were used for the other 10 trials (novel condition). For each repetition-status condition, the category member belonged to the category for half of the trials (match condition), whereas on the other half of trials, a category member from a different category was presented (mismatch condition). Category members never repeated within a block of 20 trials. Category members for the repeated-mismatch condition belonged to categories that did not appear either as a category name or member on any of the other 19 trials within a block. Critically, category members for the novel-mismatch condition belonged to the repeated category. Without this stipulation, the correct response would have been "match" whenever a member of the repeated category appeared.

The experiment included three sets of 16 blocks in which different categories served as the repeated category. Thus, all category names and members appeared equally often. Prior to these 48 blocks, there were 2 practice blocks that used different category names and members that never appeared again in the experiment.

MEG recording

Magnetic signals were measured using a 157-channel whole-head axial gradiometer system (Kanazawa Institute of Technology, Kanazawa, Japan). Five electromagnetic coils were attached to the participant's head prior to MEG recording to check head position within the MEG chamber. The locations of the coils were determined with respect to three anatomical landmarks (nasion, left and right preauricular points) on the scalp using three-dimensional digitizer software (Source Signal Imaging, La Mesa, CA) and digitizing hardware (Polhemus, Colchester, VT). The coils were localized with respect to the MEG sensors, both at the beginning and end of the experiment.

Before the visual-word experiment, participants listened to 100 repetitions of 50-ms sinusoidal tones at 250 HZ and 100 repetitions of the same tones at 1 kHz (with interstimulus intervals randomized between 750 and 1,550 ms). Auditory evoked responses to the onset of these pure tones were examined, and the auditory M100 was identified. The auditory M100 is a prominent and robust response, apparent around 100 ms after auditory onset and has been the most investigated auditory MEG response (Roberts, Ferrari, Stufflebeam, & Poeppel, 2000). A dipole-like pattern (i.e., a source-and-sink pair) in the magnetic topographic map distributed over the temporal region of each hemisphere was identified for each participant. These auditory dipole patterns were used to verify whether participants were in the proper position.

The MEG data were acquired with a sampling rate of 500 Hz, filtered on-line between 1 Hz and 200 Hz, with a notch at 60 Hz. Raw data were noise-reduced off-line using a time-shift principal-component-analysis method (de Cheveigné & Simon, 2007).

MEG preprocessing

A 1,000-ms period starting with the category-name onset was analyzed separately for the repeated and novel conditions. A second 1,000-ms period starting with the category-member onset was analyzed separately for each of the four conditions (repeated match, repeated mismatch, novel match, novel mismatch). Responses were low-pass filtered with a cutoff frequency of 20 Hz, and responses with amplitudes greater than 3 pT (~5%) were considered artifacts and discarded. Because the first trial of the repeated condition was not in fact a repeat, the first trials of both the repeated and novel conditions were eliminated from analysis. The second to tenth trials in each condition were divided into thirds according to the number of prior repetitions they contained (1–3, 4–6, 7–9). The M100, M170, and M400 responses to the category name, matching category member (e.g., "fruit-apple"), and mismatching category member (e.g., "fruit-eagle") were measured as the average of a 22-ms period centered on a time determined separately for each individual and waveform using the root mean square across all sensors to the category name, collapsed across conditions.

MEG response magnitude

On the basis of the preprocessed topographic patterns, we determined a measure of response magnitude for each waveform with a multivariate technique (Tian & Huber, 2008). Because an apparent change in magnitude might instead reflect different neural sources in different conditions, topographic similarity among conditions was evaluated using an angle test to infer whether the underlying neural-source distributions differed among conditions. The response topographies were treated as high-dimensional vectors (with the number of dimensions equal to the number of sensors), and the cosine of the angle between vectors in different conditions was calculated and compared with the cosine of the angle when comparing vectors sampled from the same condition. If no differences were found, response magnitude was measured with a projection test by mathematically projecting (i.e., calculating the dot product of) the vector from each condition onto a standard reference topography, determined by each participant's M100, M170, or M400 response to the category names (refer to the Supplemental Material available online for additional details). These techniques have proven to be useful and reliable in previous electrophysiological studies (Davelaar, Tian, Weidemann, & Huber, 2011; Huber et al., 2008; Tian & Huber, 2008; Tian & Poeppel, 2010, in press), and a free toolbox for implementing these analyses is available online (Tian, Poeppel, & Huber, 2011).

DCM

DCM was used to directly assess connectivity as a function of prior repetitions. DCM is a mathematical method that estimates connection efficiency between regions of interest (Friston, Harrison, & Penny, 2003). It assumes that external input induces activity perturbation only at particular specified regions (e.g., sensory) and that neural activity in all areas results from bidirectional interaction between connected regions. The connections among different regions are mathematically modeled through the causal influence of one neural region on another using bilinear estimation. DCM was first applied to hemodynamic responses in functional MRI (Friston et al., 2003) and later extended to event-related electrophysiological responses (David et al., 2006) by including a three-layer neural-mass model to simulate neural activity. DCM approximates the dynamics of neural activity in source space, which are estimated by temporally inverting a spatial forward model and by adjusting the connection strengths among the predetermined regions of interest (Kiebel, Garrido, Moran, Chen, & Friston, 2009). Three sets of connection-strength parameters are estimated: (a) external inputs to the neural system, (b) connections among regions of interest, and (c) modulation parameters that vary connection strengths as a function of experimental manipulations.

Results

Identifying the cortical network

DCM was used to determine the connectivity pattern and source activity for a set of regions assumed to underlie reading. Average evoked responses (Fig. 2a) revealed three different sources based on topography (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999) and timing (Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999), which have been labeled the M100, M170, and M400 in the literature. However, there are at least four levels of processing for word reading, including low-level visual information in primary visual cortex (V1; Hubel & Wiesel, 1962), the identification of orthography in the visual word-form area (VWFA; Cohen et al., 2000; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; McCandliss, Cohen, & Dehaene, 2003; Nobre, Allison, & McCarthy, 1994), lexical-semantic access in the left middle temporal gyrus (MTG; Lau, Phillips, & Poeppel, 2008), and context-dependent integration in the inferior frontal gyrus (IFG; Brown & Hagoort, 1993; Kutas & Federmeier, 2000). Assuming the reading network includes bilateral V1, bilateral VWFA, left MTG, and left IFG (see Table S6 in the Supplemental Material for locations in Montreal Neurological Institute space), we identified 24 plausible cortical networks that differed in their assumed connectivity among regions (Figs. S1 and S2 in the Supplemental Material). The most likely cortical network for these data, as determined by Bayesian model selection, contained forward and lateral connections (Fig. 2b). Remarkably, the synaptic-depression model simulation (Fig. 1b) that used previously published parameters was similar to the DCM-determined source activity of the first three stages of reading (Fig. 2b), with V1 and VWFA reaching peak responses just before and after 100 ms, respectively, whereas MTG reached its peak response just prior to 200 ms. On the basis of the similarity between the neural-network predictions and the DCM results, and on the basis of a comparison between source activity and the timing of the M170, we hypothesized that the M170 reflects semantic access in the left MTG.

The behavioral results suggested connectivity reduction between orthography and semantics. Therefore, we predicted connectivity reduction between the left VWFA (orthography) and the left MTG (semantics). According to this account, the semantic M170 response should diminish with each additional repetition (e.g., a repetition-suppression effect; Fiebach, Gruber, & Supp, 2005) owing to the reduction of input from orthography. The M400 is sensitive to unexpected lexical-semantic events (Halgren et al., 2002; Kutas & Hillyard, 1980) and has been found to underlie change detection in a reading task (Davelaar, et al., 2011). We hypothesized that the IFG makes an important contribution to the M400 response by monitoring the amount of additional semantic activation necessary to detect semantic novelty. We predicted that with increasing repetitions, (a) the M170 and the M400 responses to the repeated category name should decrease, (b) the M170 response to a matching category member should be unaffected, and (c) the M400 response to a matching category member should increase.

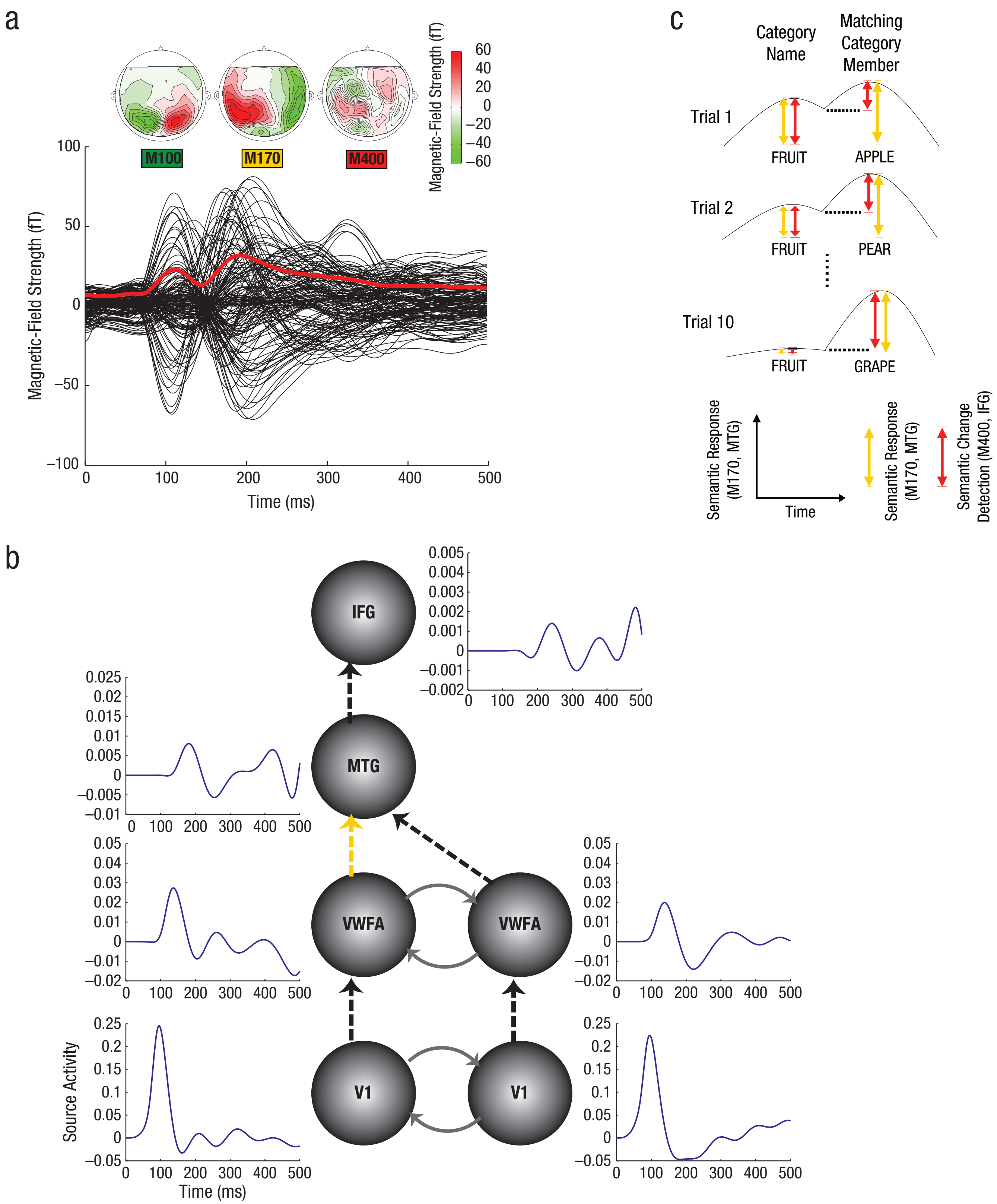

Fig. 2. Event-related responses, source activity, and predictions for the category-matching task. The graph in (a) shows waveform responses in all 157 channels (black lines) and root-mean-square average magnetoencephalography responses (red line) to the presentation of a category name, collapsed across all conditions. The topographic maps show magnetic-field strength for the three responses of interest. The connectivity in the network shown in (b) was identified using dynamic causal modeling. Source activity for each component is shown in the adjacent graph. The yellow dashed arrow shows the connection predicted to underlie semantic satiation by previous behavioral studies using the category-matching task (Tian & Huber, 2010); dashed arrows show forward connections, whereas the curved solid arrows show bilateral connections between hemispheres. The model predictions (c) show that, assuming the M170 reflects semantic activity in the left medial temporal gyrus (MTG) and the M400 reflects semantic-change detection in the left inferior temporal gyrus (IFG), both the M170 and the M400 decrease after the presentation of a repeated category name (as illustrated by the difference in the length of the arrows for Trial 1 versus Trials 2 and 10). In response to successive matching category members, the M400 increases, reflecting enhanced change detection. V1 = bilateral primary visual cortex; VWFA = bilateral visual word-form area.

The first prediction reflects connectivity reduction between orthography and semantics, the second reflects use of a nondepleted connection, and the third reflects enhanced change detection for a matching category member. Finally, note that no effects were predicted for the mismatching category member, which indicates that the behavioral results are due to the match trials rather than the mismatch trials.

MEG response magnitude

The angle test did not reveal any topographic differences in response to category names and category members (see Tables S1 and S2 in the Supplemental Material). This finding suggests similar neural-source distributions when comparing responses to the repeated and novel conditions as a function of prior repetitions. Therefore, the projection test was used to measure response magnitude (Fig. 3a). Statistical reliability of response magnitude was assessed with 2 (repetition effect: repeated vs. novel) × 3 (number of prior repetitions: 1–3, 4–6, 7–9) repeated measures analyses of variance. In response to the category name, these factors interacted for both the M170, $F(2, 24) = 4.33$, $p = .03$, and the M400, $F(2, 24) = 4.35$, $p = .02$ (see also Table S3 in the Supplemental Material). As predicted, linear contrasts revealed that both the M170

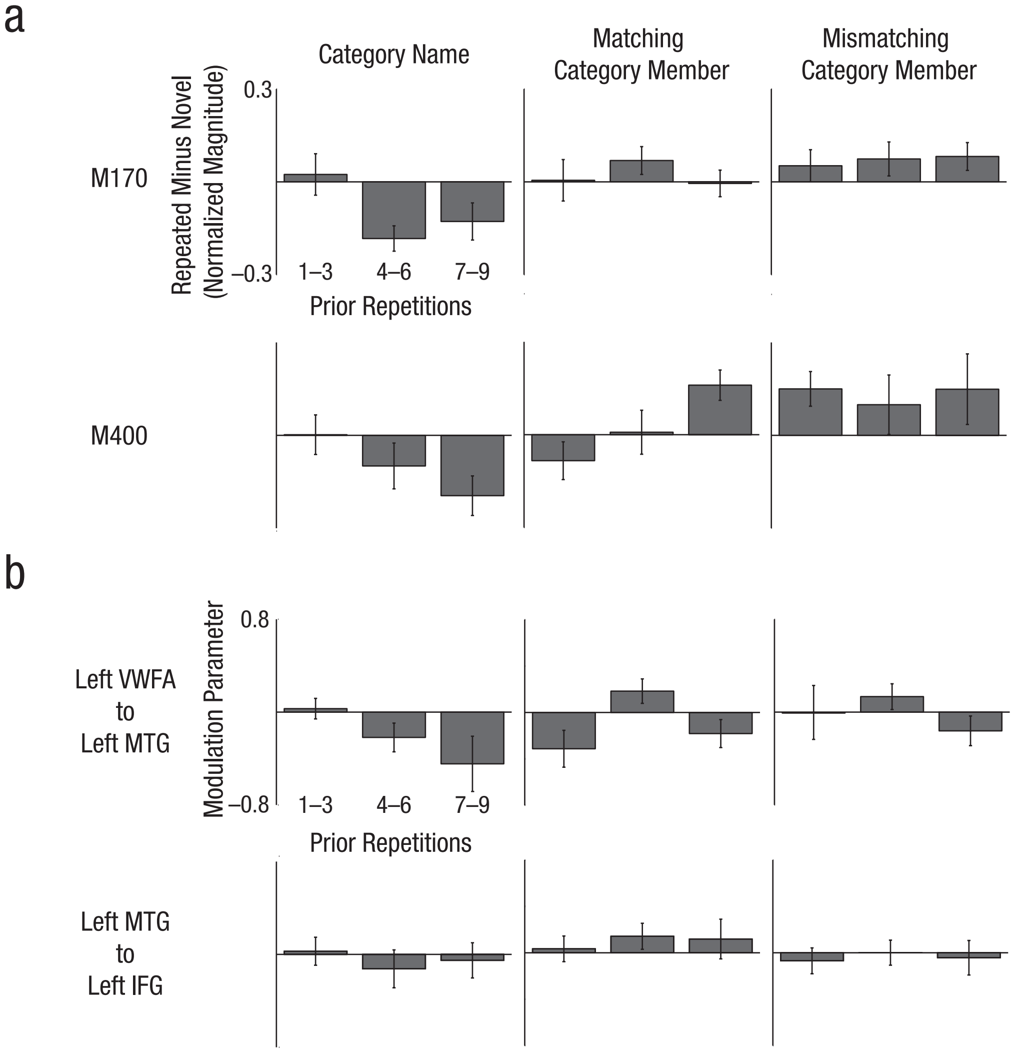

Fig. 3. Repetition effects as a function of the number of prior repetitions divided into thirds. Based on a multivariate analysis, the graphs in (a) show the difference between responses in the repeated and novel conditions to the category names, matching category members, and mismatching category members. Results are shown separately for the M170 and M400 components. Based on dynamic causal modeling, the graphs in (b) show modulation parameters, which are the difference in connectivity between the repeated-category condition and the novel-category condition. Modulation parameters are shown separately for connectivity between the left visual word-form area (VWFA) and the left medial temporal gyrus (MTG) and between the left MTG and left inferior temporal gyrus (IFG). From left to right, the graphs show results for category names, matching category members, and mismatching category members. Error bars show ±1 *SEM*.

and the M400 repetition effects to the category name decreased with increasing prior repetitions, $t(12) = 2.43$, $p = .03$ and $t(12) = 3.23$, $p = .007$, respectively. In response to a matching category member, repetition effect and number of prior repetitions did not interact for the M170 ($F < 1$), but they did interact for the M400, $F(2, 24) = 3.74$, $p = .04$ (Table S4 in the Supplemental Material): As predicted, the M400 repetition effect increased with increasing prior repetitions, $t(12) = 2.93$, $p = .01$. Finally, in response to a mismatching category member, repetition effect and the number of prior repetitions did not interact for either the M170 or the M400 (Fs < 1; Table S5 in the Supplemental Material).

Connectivity analyses

The response-magnitude analyses indirectly assessed connectivity reduction by determining whether the receiving brain region (i.e., the left MTG) could still receive, as revealed by increased semantic novelty (measured by the M400 response) for a similar word presented after the repeated word. To reinforce this conclusion, we directly tested connectivity reduction based on the electrophysiological response to the repeated category name. This was done using DCM, which calculated a modulation parameter reflecting the change in connectivity between the repeated and novel conditions. Figure 3b shows the modulation parameters for the connection between left VWFA and left MTG and between left MTG and left IFG as a function of prior repetitions. For the connections shown in Fig. 3b, the only significant change (see also Supplementary Results and Tables S7–S9 in the Supplemental Material) with increasing numbers of prior repetitions was decreasing connectivity between the left VWFA and left MTG in response to the repeated category name, $t(12) = 2.43$, $p = .03$. This identifies connectivity reduction between a brain region associated with orthography and one associated with semantics as the cause of the reduced M170 and M400 responses for a repeated word.

Discussion

Unlike suppression of the underlying representations, synaptic depression selectively removes a subset of connections, reducing prior and ongoing perceptions to enhance change detection. Although minimally disruptive, this mechanism operates at a cost, producing repetition blindness and semantic satiation, and, as shown in the present experiment, making people overly sensitive to the semantic change between words. We conclude that the apparent reduction of meaning in semantic satiation is due to a reduced connection between the word form (e.g., orthography) and the meaning of the repeated word. Thus, repeating the word "duck" reduces its meaning. However, the meaning of "duck" is not suppressed or unavailable and is immediately replenished by considering a closely related word, such as "goose."

Our study is not the first to identify connectivity reduction as an underlying cause of change detection. For instance, applying DCM to electroencephalographic responses in an auditory-oddball paradigm, researchers have found that connectivity reduction contributes to mismatch negativity (Garrido, Kilner, Kiebel, & Friston, 2009). However, our study is the first in which connectivity analyses have been used to examine the cause of high-level semantic change detection. Our findings demonstrate that connectivity reduction is a general mechanism for enhancing change detection. But why is semantic change detection desirable on the timescale reported here? It has been suggested that connectivity reduction produces context-sensitive reset in speech and language (Grossberg & Myers, 2000). For instance, the topic of discourse tends to change with each paragraph (Landauer & Dumais, 1997), and semantic responses need to be sensitive to the onset of each new topic. More generally, these results demonstrate that connectivity fluctuations can underlie basic cognitive functions, such as change detection. This claim was supported through a combination of computer simulations that make predictions regarding the functional mapping between behavior and neurodynamics and connectivity analyses of electrophysiological data (e.g., DCM) that test these predictions.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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