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Report

Stimulation of Category-Selective Brain Areas Modulates ERP to Their Preferred Categories

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Summary

Neural selectivity to specific object categories has been demonstrated in extrastriate cortex with both functional MRI [1–3] and event-related potential (ERP) [4, 5]. Here we tested for a causal relationship between the activation of category-selective areas and ERP to their preferred categories. Electroencephalogram (EEG) was recorded while participants observed faces and headless bodies. Concurrently with EEG recording, we delivered two pulses of transcranial magnetic stimulation (TMS) over the right occipital face area (OFA) or extrastriate body area (EBA) at 60 and 100 ms after stimulus onset. Results showed a clear dissociation between the stimulated site and the stimulus category on ERP modulation: stimulation of the OFA significantly increased the N1 amplitude to faces but not to bodies, whereas stimulation of the EBA significantly increased the N1 amplitude to bodies but not to faces. These findings provide the first evidence for a specific and causal link between activity in category-selective networks and scalp-recorded ERP to their preferred categories. This result also demonstrates that the face and body N1 reflects several nonoverlapping neural sources, rather than changes in face-selective mechanisms alone. Lastly, because early stimulation (60–100 ms) affected selectivity of a later ERP component (150–200 ms), the results could imply a feedforward connection between occipital and temporal category-selective areas.

Results

To examine whether there is a causal relationship between neural activity in category-selective areas in extrastriate cortex and scalp-recorded evoked potentials to their preferred categories, we first scanned subjects to individually define their occipital face area (OFA) and extrastriate body area (EBA) (see Figure 1 for a representative subject). In a separate session, we delivered transcranial magnetic stimulation (TMS) over the functionally defined right OFA and right EBA while simultaneously recording EEG data. Event-related potential to faces and headless bodies were measured. We used a double-pulse TMS protocol in which pulses were applied on each trial at 60 ms and 100 ms after stimulus onset [6, 7]. A control condition containing the same number of trials as each of the two stimulation conditions but with no TMS application (a no-TMS condition) served as baseline of a visual-only ERP response (see Experimental Procedures). Electrodes showing a clear N1 component for faces and bodies are located over the occipito-temporal scalp [5, 8]. Because OFA and EBA are located in the lateral-occipital cortex, the stimulating coil lies directly above or in proximity to the electrodes of interest (P8, PO8, and P10). As a result, these channels are affected by high-amplitude artifacts that largely outlast the immediate-pulse artifact and override the cortical evoked responses up until ~300 ms after stimulus onset (Figure S1A in the Supplemental Information available online). To recover the neural activity in all channels, we followed the subtraction technique originally proposed and validated by Thut and colleagues [9] and later used in several TMS-ERP studies (e.g., [10, 11], see Experimental Procedures for details).

ERP Results

N1 Amplitude

In previous studies, the face-selective N1 has been termed the N170, whereas the N1 for bodies has been labeled the N170 by some [12–14] or the N190 by others [3, 5] because its peak was slightly later than the face N170. In this report we will use the general term N1 for both stimulus categories. Faces and bodies elicited a strong N1 response at occipito-temporal sites P8, PO8, and P10, as commonly reported (see [8] for a review). We ran a 3 × 2 repeated-measures ANOVA on the N1 peak amplitude by using TMS site (OFA, EBA, and no TMS) and stimulus category (face and body) as factors for each of the three electrodes of interest (P8, PO8, and P10). All three electrodes showed a significant category effect due to a larger N1 amplitude to faces than to bodies (P8:$F_{(1,15)}$ = 36, $p < 0.001$. PO8: $F_{(1,15)} = 80.26$, $p < 0.001$. P10: $F_{(1,15)}$ = 20.43, $p < 0.001$). Importantly, channels P10 and PO8 also showed a significant interaction between TMS site and stimulus category (PO8: $F_{(2,30)} = 7.35$, $p < 0.01$, $\eta^2 = 0.36$. P10: $F_{(2,30)} = 9.62$, $p = 0.01$, $\eta^2 = 0.59$. P8: $F_{(2,30)} < 1$). In electrode P10 this interaction reflects a double dissociation between the face N1 and the body N1 after stimulation of their respective regions of interest; the N1 amplitude to faces was larger after OFA stimulation than after EBA stimulation ($t_{(15)} = 2.86$, $p < 0.05$, $\eta^2 = 0.36$) or the no-TMS condition ($t_{(15)} = 2.59$, $p < 0.05$, $\eta^2 = 0.31$), whereas the N1 to bodies was larger after EBA stimulation than after OFA stimulation ($t_{(15)} = 2.44$, $p < 0.05$, $\eta^2 = 0.28$) or the no-TMS condition ($t_{(15)} = 2.90$, $p < 0.05$, $\eta^2 = 0.36$) (see Figure 2). In the adjacent electrode PO8 the interaction was due to the face N1's being larger after the OFA than EBA ($t_{(15)} = 2.22$, $p < 0.05$, $\eta^2 = 0.25$) and no-TMS ($t_{(15)} = 2.73$, $p < 0.05$, $\eta^2 = 0.33$) stimulation conditions, whereas there were trends in the expected direction for larger N1 peak for bodies after the EBA than after OFA stimulation conditions ($p = 0.15$) or when no TMS was delivered ($p = 0.06$). Channel P8, although highly selective to faces, did not show a TMS effect. Overall, effects of stimulation of the face and body areas were both observed in one channel (P10) rather than distributed across different channels. This pattern can also be observed in the scalp topographies presented in the Supplemental Information (Figure S2).

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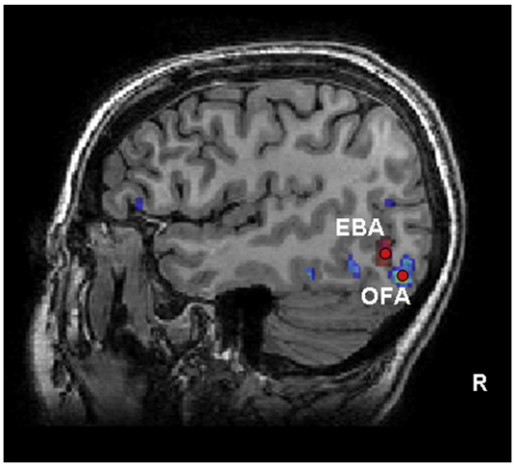

Figure 1. Occipital Face- and Body-Selective Areas

Functionally defined OFA and EBA in a representative subject. Areas are shown here in the same image to demonstrate the relative proximity to each other.

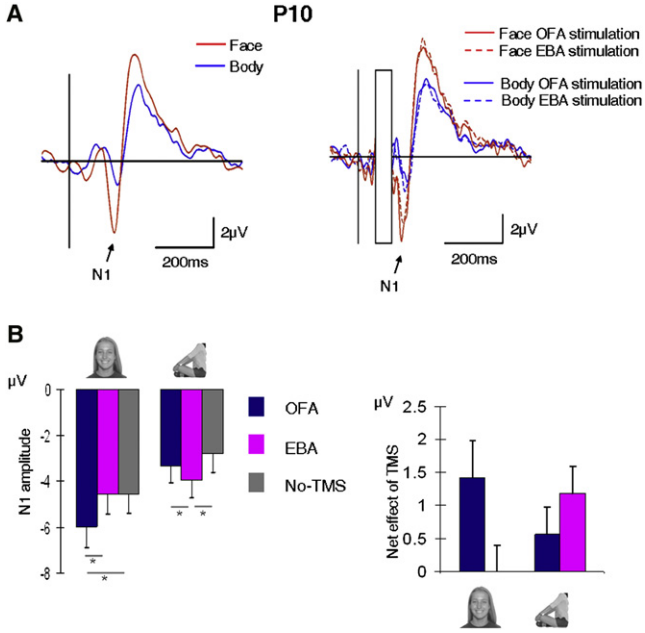

Figure 2. ERP to Faces and Headless Bodies

(A) ERP to faces and bodies in right occipito-temporal electrode P10. Left: no-TMS condition. Right: OFA and EBA stimulation conditions.

(B) Left: peak amplitude of the N1 component in electrode P10. Error bars indicate the SEM. Right: the net effect of stimulation on the N1 peak amplitude in electrode P10, after subtraction of the no-TMS N1 peak (baseline) from the N1 of each TMS condition, on an individual-subject basis. See Figure S2 for scalp topographies.

To illustrate the effect of stimulation on the ERP response, we also calculated the contribution of TMS after subtracting a baseline visual response (i.e., no-TMS condition) in electrode P10 for each participant (N1 to stimulus + TMS – [N1 to TMS alone + N1 to stimulus alone]). This index reflects the net signal modulation due to magnetic stimulation [11] (Figure 2B).

N1 Latency

The N1 recorded for bodies peaked approximately 15 ms later than the face N1 in all electrodes of interest, as previously reported [5]. Repeated-measures ANOVA on the peak latency revealed a main effect of category in each electrode (P8: $F_{(1,15)} = 13.94$, $p < 0.01$. PO8: $F_{(1,15)} = 31.93$, $p < 0.0001$. P10: $F_{(1,15)} = 12.46$, $p < 0.01$), but no effect of stimulation site (all p values > 0.2) or interaction (all p values > 0.2) (see Table 1 for P10 values and Figure S2 for scalp topographies for faces and bodies across different latencies).

The specific effects generated by OFA and EBA stimulations on the ERPs to their preferred categories were restricted to the stimulated hemisphere. Examination of occipito-temporal electrode sites over the nonstimulated left hemisphere (P7, PO7, and P9) revealed that N1 amplitude was higher for faces than bodies (P7: $F_{(1,16)} = 30.56$, $p < 0.0001$. PO7: $F_{(1,16)} = 16.1$, $p < 0.01$. P9: $F_{(1,16)} = 27.05$, $p < 0.0001$), but no effect of stimulation site and no interaction were found (all p values > 0.3). The N1 peak latency over the left hemisphere presented a similar pattern to the one observed over the right hemisphere: there was a significantly later peak for bodies than for faces (P7: $F_{(1,16)} = 47.28$, $p < 0.0001$. PO7: $F_{(1,16)} = 38.73$, $p < 0.0001$. P9: $F_{(1,16)} = 19.55$, $p < 0.001$). There was neither an effect of stimulation site nor an effect of interaction (all p values > 0.05) of site and category.

Vertex Positive Potenrial

To further assess the specific effects of TMS to OFA and EBA on face and body processing, we sought to examine the vertex positive potential (VPP), a face-selective ERP component that is maximal at central channel Cz, farther from the stimulated occipital cortex [15, 16]. The neural sources of the VPP were claimed to be the same sources that generate the right and left occipito-temporal face-selective N170 [16, 17]. Therefore, we expected to observe at the VPP the same pattern of results that we found in the occipito-temporal channels. However, because both hemispheres contribute to the centrally recorded VPP and we only stimulated the right hemisphere, we predicted that the VPP would show a weaker effect of stimulation relative to the effect we found in the right occipito-temporal channels. A 3 × 2 ANOVA with site and category revealed a main category effect ($F_{(1,16)} = 82.22$, $p < 0.001$) due to higher VPP amplitude to faces than bodies and a significant interaction between site and category ($F_{(2,32)} = 6.3$, $p = 0.005$, $\eta_p^2 = 0.46$). Simple effects showed amplitude enhancement for each object category after stimulation of its selective area relative to stimulation of the other area or to no TMS: VPP amplitude for faces was higher after OFA than EBA ($t_{(16)} = 2.11$ $p = 0.05$ $\eta^2 = 0.22$) or no-TMS stimulation conditions ($t_{(16)} = 2.51$, $p < 0.05$, $\eta^2 = 0.28$) . VPP for bodies was higher after EBA than OFA stimulation conditions ($t_{(16)} = 2.1$, $p = 0.05$, $\eta^2 = 0.22$) although not after the no-TMS condition ($p = 0.23$) (See Figure S1B).

Discussion

The representation of visual stimuli by specialized category-selective mechanisms is a well-established organizational principle of high-level visual cortex (for review, see [2]). Similarly, the selectivity of the scalp-recorded N1 component at occipito-temporal sites to faces and bodies is well-established [4, 8, 12, 14, 18–20]. In an attempt to suggest possible sources for the face or body ERP response, past studies applied methods of source estimation for the category-selective N1 [5, 21, 22]. Other studies linked ERP and fMRI selectivity by correlating ERP with fMRI measures across subjects [23, 24] or examined the similarity of the effects of specific experimental manipulations on the ERP and fMRI responses at the

Table 1. Amplitudes and Latencies of the N1 Peak in Occipito-Temporal Electrodes after OFA Stimulation, after EBA Stimulation, and in the No-TMS Control Condition

	Face			Body			Face			Body		
	OFA	EBA	No TMS	OFA	EBA	No-TMS	OFA	EBA	No TMS	OFA	EBA	No TMS
	Right Hemisphere (P10)						Left Hemisphere (P9)					
Amplitude (μV)	−5.99 ± 0.75	−4.56 ± 0.66	−4.57 ± 0.61	−3.34 ± 0.38	−3.96 ± 0.49	−2.79 ± 0.48	−4.53 ± 0.44	−4.47 ± 0.46	−3.93 ± 0.43	−2.89 ± 0.58	−2.74 ± 0.58	−2.58 ± 0.38
Latency (ms)	156.1 ± 4.41	153.7 ± 3.59	152.6 ± 3.28	173 ± 5.49	177 ± 4.44	172.6 ± 4.56	160.7 ± 4.15	153 ± 3.66	160.2 ± 4.51	176.8 ± 4.17	173.5 ± 4.7	173.4 ± 4.67
	Right Hemisphere (PO8)						Left Hemisphere (PO7)					
Amplitude (μV)	−9.5 ± 1.39	−7.97 ± 1.39	−7.92 ± 1.27	−3.72 ± 1.41	−4.96 ± 1.44	−3.11 ± 1.23	−7.06 ± 1.37	−6.85 ± 1.27	−6.57 ± 1.12	−4.01 ± 0.99	−3.83 ± 0.84	−3.79 ± 1.03
Latency (ms)	155.9 ± 3.03	158.7 ± 3.92	158.1 ± 2.8	164 ± 3.92	171.1 ± 4.86	169.6 ± 3.55	156.6 ± 2.87	157.3 ± 3.14	157.9 ± 2.7	168.8 ± 3.49	169.2 ± 4.01	174.6 ± 2.94

Standard errors of the mean are indicated beneath each value. See also Figure S1.

group level [20, 25]. However, no study has yet manipulated neural activity in category-selective areas and directly measured the impact on ERP selectivity to these categories. By disrupting functionally defined object-selective areas with TMS and measuring the subsequent modulation in ERP to their preferred categories, we revealed a *causal* link between neural activations in category-selective networks and scalp-recorded potentials. The main finding was that stimulation to the occipital face area significantly enhances the N1 response to faces but not to bodies, whereas stimulation to the extrastriate body area significantly enhances the N1 response to bodies but not to faces. A similar double dissociation was also found in the VPP, which is believed to reflect the same neural sources that generate the N1 [16, 17]. These findings provide the first evidence that neural activation in the face and body extrastriate networks is causally and specifically related to scalp-recorded electrical responses to their preferred stimuli.

In addition to the double dissociation in the N1 and VPP, two additional findings support our conclusion that the effect of TMS was specific to the stimulated category-selective networks. First, relative to faces, bodies produced a delayed N1 component, as previously reported [5] (but see [14]). Importantly, this latency difference was not modulated by TMS. That is, although the magnetic pulses were given at the same latency (60 ms and 100 ms) for both sites, they did not generate their effect on the N1 at the same latency. Instead, each TMS condition had a maximal effect at the latency at which N1 to its preferred stimulus peaks when no stimulation is given (Figure S2). These findings suggest that stimulation at each site affected a separate network. Second, results also showed that the double dissociation of the face and body N1 after TMS to the right OFA and right EBA did not propagate to the left hemisphere, implying that it was localized to the stimulated hemisphere.

The category-specific effect of stimulation on the N1 amplitude raises the question of whether the OFA and EBA themselves are sources of the face and body N1. The current study cannot answer this question directly, but in light of previous findings regarding the timing of face-selective brain activations, we propose that the OFA and EBA are not the direct sources for the N1 component. In two prior TMS studies, stimulation of the OFA impaired face discrimination when it was delivered at 60–100 ms, but not when it was delivered during later latencies up to 290 ms (i.e., not at the N170 time window) [6, 7]. Similarly, in a simultaneously combined EEG-fMRI investigation, a high correlation was found between face selectivity in the OFA and ERP face selectivity around 100 ms, whereas the N170 face selectivity was not correlated with the OFA face selectivity but with face selectivity in the more anterior face areas in the temporal cortex: the FFA (fusiform face area) and pSTS (posterior superior temporal sulcus) [24]. In the current study TMS was administered at 60 and 100 ms, which is earlier than the N1 latency and might coincide with information processing within the OFA. We therefore suggest that the magnetic stimulation modulated neural output from the OFA to face-selective areas in the temporal cortex, which in turn, directly contributed to the N1 component. This suggestion is also compatible with the idea that TMS induces an excitatory effect on neural output [26, 27]. Thus, the TMS effect on the subsequent N1 suggests connectivity between occipital and more anterior mid-temporal areas within the face network. Note that the same idea might apply to the VPP, which is considered to be the central counterpart of the N1 [15–17]. These findings might be in line with the influential theoretical model of neural face network that was suggested by Haxby and colleagues. This model proposes feed-forward connections within the core face-processing system from the OFA to both the FFA and pSTS in the temporal lobe [28].

The body-selective EBA is also located in the occipital lobe, in close proximity to the OFA (Figure 1). Although there are currently no published data showing that the EBA processes body stimuli during the same time window the OFA does, given the great proximity between the two lateral-occipital areas (see Figure 1), it is plausible that the EBA operates at a similar latency as the OFA. Recently, two TMS studies reported impaired body discrimination when TMS was applied to the EBA [29, 30]. In these studies the EBA was stimulated 150–250 ms after stimulus onset. However, this late stimulation latency took place during the blank period between the sample and probe stimuli rather than concurrently with the presentation of a stimulus and therefore probably disrupted a mnemonic trace of the probe stimulus rather than its initial visual processing. We therefore suggest that, similar to results for the OFA condition, the effect of EBA stimulation on the N1/VPP response reflects activity modulation at the body-selective cortex in mid-temporal lobe and not in the occipital lobe. We note again that this interpretation is based on indirect evidence but could have found direct support had it been possible to directly stimulate the mid-temporal face and body areas located deep within the ventral temporal lobe.

In previous TMS studies, face and body discrimination was impaired by TMS delivered over the OFA and EBA [7, 31], whereas ERP amplitudes in this study were enhanced. Although it might seem contradictory, impaired performance might be associated with enhanced, rather than reduced, ERP amplitude, as demonstrated by ERP studies of the face-inversion effect. Inversion of a face image significantly reduces recognition abilities [32, 33] but increases the amplitude of the N170 in relation to upright faces [4, 32–35]. Furthermore, the lower performance to inverted faces was found to correlate with the degree of N170 enhancement [36]. Thus, enhanced ERP amplitude might be associated with poor task performance. Furthermore, consistent with the enhancing effect of TMS on the ERP amplitude, as revealed here, a recent study that applied TMS concurrent with recording of visual evoked potentials reported an increase in visual scalp-recorded potentials as a function of the magnitude of stimulation [11]. In light of these considerations, it is likely that local neural excitability driven by the preferred input to the stimulated site (faces in the OFA, bodies in the EBA) at the time of magnetic stimulation gave rise to increased response only to that preferred category. Even though it is still unclear how exactly TMS modulates the neural signal, this modulation of activity will be suboptimal for intact behavioral performance because it is not directly driven by stimulus-encoding demands.

A well-established finding in ERP studies is that the amplitude of the N1 is higher for faces than for nonface categories, including headless bodies, as our findings also show. This observation has two possible accounts. According to one alternative, the lower N1 amplitude to bodies than faces reflects the lower response of face areas to nonpreferred body stimuli. According to a second possibility the N1 to bodies reflects the response of body-selective areas to their preferred category, and the lower amplitude may be due to their different locations, orientation or type of neural activity (see for example [20]). The specificity of the TMS effect as a function of the stimulated area implies that the N1 response to the different categories reflects activity in distinct networks, rather than activity change within the face network only. In other words, our findings support the second alternative suggesting that the lower N1 amplitude to bodies reflects the contribution of neural activity at body-selective areas rather than the lower response to non-preferred body stimuli by the face area alone.

In summary, this study shows for the first time a causal link between category-selective areas revealed with fMRI and selectivity of scalp-recorded ERPs to their preferred category. Specifically, it demonstrates that ERP to faces and bodies is directly related to neural activity in the functionally defined face- and body-selective networks. Results also suggest a feed-forward connection between occipital and temporal areas within the face and body networks in the human visual cortex.

Experimental Procedures

Participants

Nineteen healthy right-handed volunteers (average age 26.6 ± 4.7 yr; 11 males) participated in the study. Two of the participants were excluded from final analysis as a result of excessive pulse-related noise that could not be reliably removed, as well as unrecognizable visual evoked potentials. No one withdrew from the experiment because of discomfort with the TMS application or for any other reason. All participants gave written informed consent, as approved by the Tel-Aviv Sourasky Medical Center, both for the MRI scan and the TMS-EEG session.

Functional MRI Scan

In order to determine the regions of interest for TMS stimulation, we had participants undergo a structural MRI scan and a functional localizer scan a few days before the TMS study. Scans were done in a 3T General Electric MRI scanner with an 8 channel head coil in the Tel-Aviv Sourasky Medical Center. High-resolution functional data were collected with echo-planar imaging with a TR of 2 s, TE of 35 ms, 22–24 slices aligned parallel to the temporal lobe (according to the sylvian fissure), matrix of 96 × 96, and FOV of 20 cm; slices were 2.4 mm thick, and there was no gap between them. Stimuli were presented with Psychtoolbox2 for Matlab [37] and projected on an MRI-compatible screen inside the scanner. Participants observed six 16 s blocks of faces, headless bodies, objects, and scrambled objects and executed a one-back task to maintain concentration on stimulus categories. About half of the participants observed six additional blocks of natural scenes, designated to be used as a localizer for a different study. Data were analyzed with SPM5 for Matlab (http://www.fil.ion.ucl.ac.uk/spm/). OFA was defined as a cluster that was located in the lateral occipital cortex and responded more to faces than to objects ($p < 0.00001$) after voxels responding more to bodies than to objects ($p < 0.01$), and vice versa for the EBA, were masked out.

Main Experimental Procedures

Participants were seated with their heads stabilized on a chinrest 50 cm from a 17″ CRT screen in a dimly lit room. A total of 300 faces, 300 headless bodies, and 60 targets (cars) were randomly presented over a white background at the center of the screen. The experiment included six blocks: two blocks for each one of the three TMS conditions (OFA stimulation, EBA stimulation, and no TMS). Block order was counterbalanced across participants. Each of the six blocks contained 50 faces, 50 bodies, 50 blanks, and 10 car targets presented in a randomized order. That is, each of the three TMS conditions comprised a total of 100 faces, 100 bodies, 100 blanks, and 20 car targets. The no-TMS condition served as a baseline (see, for example, [31]), as described in the Results. Stimuli occupied ~6° × 8° of visual angle and remained on the screen for 250 ms with an inter-stimulus interval (ISI) of 1000 ms. A 0–500 ms random jitter was added to the ISI so that participants could not anticipate the pulses. On the basis of previous TMS studies of face perception that examined the latency during which the OFA processes faces [6, 7], two TMS pulses (a double-pulse stimulation procedure) were delivered at 60 and 100 ms after stimulus onset. So that a residual pulse-noise template for subtraction could be calculated, a total of 300 blank-screen trials were randomly presented. On each blank trial (TMS only), two-pulse TMS was also delivered, as was the case with face, body, and target trials. Participants were instructed to respond to target car stimuli by pressing a key. The task was chosen so that participants would remain alert to stimulus categories and so that motor responses would be minimized. Because movements result in small shifts in the location of the magnetic field, small movements change the form of the noise induced to the EEG channels. It was therefore crucial in our combined EEG-TMS procedure to minimize movements in order to establish an accurate noise template for the subtraction technique. Therefore, a target-detection task with rarely occurring targets (cars) was chosen.

TMS Stimulation and Target-Site Localization

We used Magstim Rapid2 stimulator (Magstim) with a 50 mm double coil. A no-TMS control condition included a coil pointing upward at 5 cm behind and to the right of the subject's head. TMS stimulation was delivered at 60% of the stimulator power for all subjects, according to procedures used in previous studies on TMS to the OFA [6, 7, 31, 38] and several other TMS investigations [39, 40]. Stimulation sites were localized with a 3D neuronavigation system (BrainSight, Rogue Research). After coregistration of the individual structural scan with the participant's head, coil locations were marked on the head based on the activation maps superposed on the structural scan. During TMS sessions the coil was stabilized by a holder.

EEG Recording and Analysis

Electroencephalogram (EEG) data were recorded with a BrainAmp MRplus amplifier (BrinProducts, GmBH) from 32 Ag/AgCl electrodes mounted on an elastic cap according to a modified 10/20 system (Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, AFz, Cz, Pz, Oz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, PO7, PO8, P9, and P10). EEG data were sampled at 5 kHz and referenced to the tip of the nose with a fronto-central (Fz) ground. Electrode wires were arranged in parallel from the right to the left side of the head so that TMS artifacts would be minimized. The amplifier and the flat cable of the channel input were covered with an aluminum blister

foil so that TMS and other sources of interference to the recorded signal would be further reduced.

EEG data were analyzed with Matlab 7.6 (MathWorks Inc) and the EEGLAB 6.03 plugin for Matlab [41]. To enable filtering, we cut the two TMS pulses from the EEG data by removing the data starting two samples prior to the first pulse and ending 16 ms after the second pulse. Continuity was then achieved by stepwise linear interpolation of values between the two edges of the cut signal (see, for example, [42]). Data were filtered with a 0.5–45 Hz band-pass filter, rereferenced to the algebraic common reference, and downsampled to 500 Hz. Blink artifacts were removed from the data via independent component analysis (ICA). Blink-related components were identified on the basis of their waveform, scalp topography, and frequency spectra and then rejected from the data. Then, epochs ranging from −100 ms to +600 ms around stimulus onset were separately extracted for each condition in each session.

Because our electrodes of interest are located at occipito-lateral sites where the coil was also located, they were affected the most by long-lasting TMS residual artifacts (see Figure S1A). To correct for these artifacts, we measured an averaged TMS-only template time locked to 60 ms before the first TMS pulse applied in the absence of visual stimulation, in trials randomly administered during each session. The resulting TMS-only epoch served as a template that could be subtracted from the visual evoked potentials in each TMS condition [9]; see also [10, 11]. This procedure was done in each session separately because the form of the artifactual activity changes from session to session (even within the same stimulation site) as a result of modifications in coil position and/or orientation. Subtraction was applied in the control no-TMS condition as well so that all conditions would be comparable. The TMS pulse latencies that were chosen to maximize impact on cognitive processes that underlie ERP selectivity (60–100 ms) override the P1 component, which could therefore not be recovered after removal of the two consecutive pulses. The time window under the double pulses was not shown or analyzed (see for example [42, 43]). In three subjects one channel was removed from analysis (in all conditions) because of uncorrectable noise or technical problems in part of the sessions. Statistical analyses were performed on Statistica 7 (StatSoft Inc). The eta squared (η^2) estimate of effect size is reported for interaction and simple effects.

Supplemental Information

Supplemental Information includes two figures and can be found with this article online at doi:10.1016/j.cub.2011.09.030.

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