

Magnetic Stimulation of Extrastriate Body Area Impairs Visual Processing of Nonfacial Body Parts

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Summary

Functional magnetic resonance imaging indicates that observation of the human body induces a selective activation of a lateral occipitotemporal cortical area called extrastriate body area (EBA) [1]. This area is responsive to static and moving images of the human body and parts of it, but it is insensitive to faces and stimulus categories unrelated to the human body [1, 2]. With event-related repetitive transcranial magnetic stimulation, we tested the possible causal relation between neural activity in EBA and visual processing of body-related, nonfacial stimuli. Facial and noncorporeal stimuli were used as a control. Interference with neural activity in EBA induced a clear impairment, consisting of a significant increase in discriminative reaction time, in the visual processing of body parts. The effect was selective for stimulus type, because it affected responses to nonfacial body stimuli but not to noncorporeal and facial stimuli, and for locus of stimulation, because the effect from the interfering stimulation of EBA was absent during a corresponding stimulation of primary visual cortex. The results provide strong evidence that neural activity in EBA is not only correlated with but also causally involved in the visual processing of the human body and its parts, except the face.

Results and Discussion

Neuropsychological and neuroimaging studies suggest that the human body is represented in brain regions that are at least partially different from those subserving the representation of noncorporeal objects [3–8] and that processing information from and about the body can be

regarded as an independent cognitive ability [9, 10]. Only recently, however, has a cortical area selectively responsive to static images of the human body or its parts been demonstrated in the lateral occipitotemporal cortex, predominantly in the right hemisphere [1]. This area, called the extrastriate body area (EBA), is activated during observation of partial or whole photographs or sketchy drawings of human bodies but not by viewing various stimulus categories unrelated to the human body [1, 2].

Further, EBA is largely insensitive to facial stimuli and, thus, may be considered a complementary counterpart of the so-called fusiform face area, a portion of the occipitotemporal cortex [11, 12], which is specifically responsive to facial stimuli but insensitive to nonfacial body parts [11]. Although damage to the latter cortical region selectively impairs performance on face recognition tasks [13], there are no studies on the possible occurrence of specific deficits in the perceptual analysis of nonfacial body parts after focal damage to the EBA region. We used event-related repetitive transcranial magnetic stimulation (rTMS), a technique that provides the unique opportunity to create temporary inactivation of cortical areas in healthy individuals [14, 15], to explore a possible causal link between interference with neural activity in EBA and impairments in the visual discrimination of body parts.

In a two-choice matching-to-sample task, 14 right-handed participants were required to decide which of two similar upper-limb images matched a single sample previously seen during a tachistoscopic exposure (Figure 1A). Photographs of face parts and motorcycle parts served as control stimuli in two matching-to-sample tasks that were comparable to the former task (Figure 1B). All the matching and nonmatching stimuli in each pair were equated for luminance and viewing perspective, and the nonmatching stimulus differed from the sample by a single or very few anatomical details in the case of limbs and faces (e.g., the shape and size of a forearm or a nose) and a single or a few structural details in the case of motorcycles (e.g., the shape and size of a handlebar). We applied rTMS trains of two pulses (10 Hz, 200 ms) over the right hemisphere 150 ms after the onset of the sample. EBA and the primary visual cortex (V1) were stimulated in different blocks, and an additional block with a control sham stimulation served as baseline (Figure 1C). Delivering two TMS pulses at critical delays after target presentation has previously proved successful for the functional inactivation of the primary visual cortex or other higher order visual cortical areas, depending on the delay magnitude [16, 17].

A two-way repeated-measures ANOVA was performed on reaction times (RTs), with stimulation site (sham, EBA, V1) and stimulus category (body parts, face parts, motorcycle parts) as main factors. Although the effects of the two main factors failed to reach significance [stimulation site: $F(2,26) = 1.2$, $p = 0.316$; stimulus category: $F(2,26) = 0.69$, $p = 0.509$], their interaction proved highly significant [$F(4,52) = 3.17$, $p = 0.021$]. Figure 2 suggests

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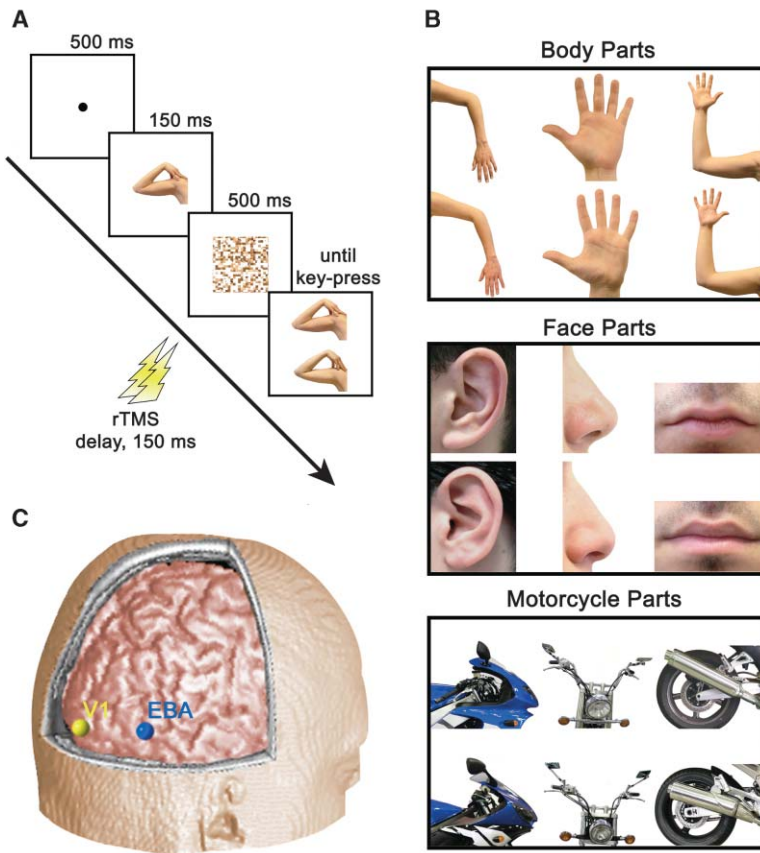


Figure 1. Time Line of the Task, Experimental Stimuli, and Stimulation Sites

(A) Schematic representation of the trial events. Repetitive transcranial magnetic stimulation (rTMS) was applied with a delay of 150 ms after sample presentation. Ten hertz trains lasting 200 ms were delivered.

(B) Examples of the experimental stimuli. Three pairs for each stimulus category are shown.

(C) Stimulation sites on a cortical model. Scalp locations corresponding to extrastriate body area (EBA) and primary visual cortex (V1) in the right hemisphere were targeted for each observer by means of the SofTatic neuronavigation system. Mean coordinates, in Talairach space [40], of the stimulation sites were $x = 51.8 \pm 0.15$, $y = -72.4 \pm 0.2$, and $z = 3.2 \pm 0.13$ for EBA, corresponding to Brodmann's area 37, in the posterior part of the middle temporal gyrus, and $x = 19.3 \pm 0.8$, $y = -98.1 \pm 0.1$, and $z = 0.7 \pm 0.3$ for V1, corresponding to Brodmann's area 17, in the middle occipital gyrus.

that the significance of the interaction was due to a longer mean RT in the EBA stimulation/body parts condition than in all other conditions of the interaction. A Tukey post-hoc test confirmed this suggestion by showing that the mean time needed to match body parts to sample was significantly longer during EBA stimulation ($953.07 \text{ ms} \pm 88.4 \text{ ms}$) than during both sham stimulation

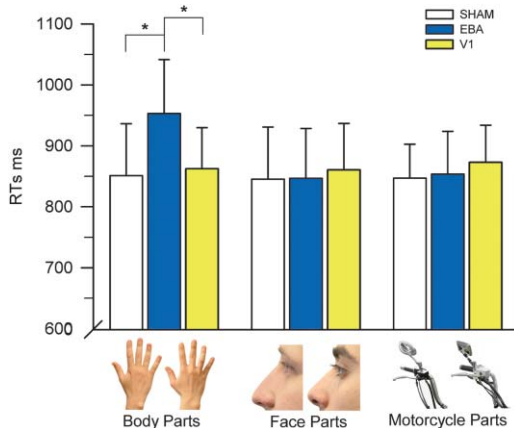


Figure 2. Mean Latencies (\pm Standard Errors) for the Three Tasks Reaction times (RTs) during sham stimulation and magnetic stimulation of extrastriate body area (EBA) and of the primary visual cortex (V1) are plotted for each stimulus category. Asterisks denote significant comparisons between the three stimulation conditions for each stimulus category.

($851.11 \text{ ms} \pm 85.03 \text{ ms}$, $p = 0.013$) and V1 stimulation ($862.29 \text{ ms} \pm 67.68 \text{ ms}$, $p = 0.04$). Further, during EBA stimulation, mean matching-to-sample RT was significantly longer with body part stimuli than with both face part stimuli ($846.86 \text{ ms} \pm 81.66 \text{ ms}$, $p = 0.008$) and motorcycle part stimuli ($853.68 \text{ ms} \pm 70.12 \text{ ms}$, $p = 0.017$). Moreover, mean RT for matching body part stimuli during EBA stimulation was significantly longer than mean RT for matching face parts during sham ($845.41 \text{ ms} \pm 85.46 \text{ ms}$, $p = 0.007$) and V1 stimulation ($860.66 \text{ ms} \pm 76.0 \text{ ms}$, $p = 0.034$) and mean RT for matching motorcycle parts during sham stimulation ($847.14 \text{ ms} \pm 55.53 \text{ ms}$, $p = 0.009$). No other orthogonal comparison within the two-way interaction proved significant ($p > 0.1$ in all cases), confirming that a significant experimental effect resulted solely from the combination of EBA stimulation with body part stimuli. The absence of significant differences during sham stimulation supports a basic similarity between the three stimulus categories in terms of task difficulty.

No apparent relation to type of task, presence or absence, and locus of rTMS stimulation was observed for percent correct responses (Table 1). A two-way repeated-measures ANOVA on percent correct responses with stimulation condition and stimulus category as main factors confirmed the absence of significant effects from either stimulation condition [$F(2,26) = 1.19$, $p = 0.32$] or stimulus category [$F(2,26) = 1.95$, $p = 0.162$] as well as from their interaction [$F(2,18) = 0.86$, $p = 0.495$].

Because both accuracy and latency in the sham stim-

Table 1. Mean Accuracy (\pm Standard Errors) for the Three Tasks during Each Stimulation Condition

	Sham	EBA	V1
Body parts	72.41% \pm 2.82%	72.45% \pm 3.43%	72.41% \pm 2.99%
Face parts	78.09% \pm 2.89%	78.76% \pm 1.95%	71.42% \pm 4.92%
Motorcycle parts	79.22% \pm 2.63%	75.74% \pm 3.23%	77.34% \pm 2.88%

ulation condition were comparable for the three stimulus categories, the latency increase in the task with body parts during rTMS of EBA could not be accounted for by a different difficulty of the three tasks. Nor could the effect be ascribed to the multicomponent structure of the body part images, a structure which may by itself act on the brain differently from single-component stimuli [18], because EBA stimulation failed to affect performance with the multicomponent motorcycle part stimuli. Moreover, the absence of any influence of EBA rTMS on matching face parts indicates that the processing of at least some biological stimuli was not affected. The effect limited to body parts was obtained with EBA stimulation but not with V1 stimulation; the latter stimulation was associated with a slight and nonsignificant RT increase with all kinds of stimuli, in agreement with previous reports of lack of visual effects when V1 is subjected to TMS stimulation 150 ms after visual target presentation (see [19]). It can thus be argued that the selective slowing of matching-to-sample RT with nonfacial body part stimuli during EBA stimulation is best attributed to the ability of rTMS to cause a short-lasting impairment of the normal activity in an area specifically devoted to this form of categorical processing. Whether the impairment was due to an interference of rTMS on the processing of the sample or the probes, on the maintenance of the sample in working memory (e.g., [20]), or on more than one or all of these processing stages cannot be presently determined on the basis of the available evidence.

Studies of patients with brain lesions have long demonstrated cognitive deficits restricted to specific stimulus categories such as, for example, living versus inanimate entities [21]. The present results suggest that lesions in the region of EBA may result in a deficit specifically affecting the perception of body parts excluding the face, in the same way as brain lesions involving the medial occipitotemporal cortex impair face recognition but not recognition of nonfacial body parts [13]. On the other hand, aspects of body knowledge different from the perceptual analysis of nonfacial body parts have been found to be specifically affected by brain lesions, particularly in the parietal lobe. Such body-related disorders include out-of-body perceptions [22], disownership of body parts [23, 24], deficits in the representation of the spatial relationships between body segments [25], and the general semantics of body structure [4, 26–28].

Functional neuroimaging studies complement data obtained from brain-damaged patients by showing, for example, that visual analysis of living objects activates different sectors of the posterior temporal lobes from those activated by inanimate objects [29]. In a similar vein, human faces selectively activate medial occipitotemporal areas [11, 12], and tasks of mental transformation of the body in space selectively activate posterior

parietal areas [5–7]. The present finding, that rTMS of EBA induces a selective impairment of processing nonfacial body parts, provides strong evidence that neural activity in this area is not only correlated with, but also necessary for, this particular aspect of body knowledge. A selective impairment in the visual processing of body parts but not of face parts is consistent with neuroimaging studies showing discrete neural representations of facial and nonfacial body parts [1, 2, 30, 31].

A region within the human superior temporal sulcus is selectively activated during observation of various forms of biological motion but not of static images of the human body [2, 32]. Cells responding to the presentation of dynamic images of body parts have been identified also in the monkey's superior temporal cortex [33], and some of these cells respond even to static images of body postures that suggest an immediate transition to motion [34]. In an earlier study [35], visual analysis of pictures of body gestures in humans induced a lateral occipitotemporal junction activation that has been attributed to an inference of motion from static body postures. Implied motion does not seem necessary for EBA responses to the human body because EBA is activated by static images of human bodies regardless of their ability to imply motion [1]. Because the present stimuli were static images of body parts matched for general posture, discrimination performance was arguably based on morphological categorization independent of posture or implied motion cues. Such categorization appears crucial for recognizing bodies and body segments across the huge variability of postures and actions made possible by articulated joints and the potential for multidirectional movements. This does not mean that bodies in action are not coded in EBA. Except in the mirror, our faces are out of view, but our limb posture and movements can be monitored by vision during both self-directed and environment-directed actions. As a consequence, the correspondence between body-related visual perception and somato-motor representations is much higher for limbs than for faces. Visual monitoring of our own body postures and actions and comparisons with those of other people interact with and reinforce the proprioceptive signals needed for the construction and maintenance of the body schema [36]. Thus, somatic information from the limbs is probably most susceptible to visual modulation contributing to body knowledge. The hypothesis of a specialization of EBA for the multimodal representation of both static and moving body parts, but not of face and head parts, is supported by the recent neuroimaging finding that self-produced movements of the limbs can modulate activity in this area, whereas self-produced movements of the eyes cannot [37]. Further studies are needed to determine the respective contributions of EBA to the representations of the motionless and moving body and to under-

stand the mutual relations between EBA and other cortical systems involved in the coding of bodily forms and bodily actions [30, 38].

Conclusion

The current results clearly show that repetitive magnetic stimulation of EBA impairs visual processing of nonfacial body parts but does not affect visual processing of face parts or noncorporeal stimuli. When considered along with previous neuroimaging evidence that EBA is activated by viewing images of the human body except faces [1, 2], our findings strongly imply that neural activity in this area is not only correlated with, but also necessary for, this specialized form of categorical visual processing.

Experimental Procedures

Participants

Fourteen healthy participants (four men and ten women) aged 20–30 (mean = 23.6) were recruited for the study. A standard handedness inventory [39] allowed us to ascertain that all participants were right-handed. They were native Italian speakers with normal or corrected-to-normal visual acuity in both eyes. None of the participants had neurological, psychiatric, or other medical problems or had any contraindication for TMS [40]. Participants were naive to the purposes of the experiment, and information about the experimental hypothesis was provided only after the experimental tests were completed. Participants gave their written informed consent, and the procedures were approved by the ethical committee of the Fondazione Santa Lucia, Rome.

Stimuli and Apparatus

Stimuli were color pictures taken with a digital camera and representing upper-limb parts, face parts, and motorcycle parts. Sixteen pairs of stimuli for each category were used. In each pair, the nonfacial and facial body stimuli were pictures of two different models assuming the same bodily posture or facial expression. Upper-limb stimuli included dorsum and palm views of different hands, entire arms, and a forearm flexed with the hand touching the shoulder. Face part stimuli included frontal and profile views of noses, lips, eyes, and ears. Motorcycle part stimuli included frontal and profile views of handlebars with rearview mirrors, front wheels with a front lamp, back wheels with a muffler, saddles, and tanks of different examples of motorcycles. Stimulus sets were balanced for sex and for laterality of the models. Participants sat 57 cm away from a 17 in monitor (resolution: 1024 × 768 pixels; refresh frequency: 99 Hz) on which stimuli appeared on a white background and subtended a 9.1° × 9.1° square region around the fovea. Stimulus-presentation timing, rTMS triggering, and randomization were controlled by a custom software created with Matlab (The MathWorks, Natick, MA) and the Psychophysics Toolbox extensions [41]. During the experiment, all participants had their chins and foreheads restrained and their heads aligned with the center of the viewing screen. Eye position was monitored, and fixation was checked continuously during tachistoscopic presentation by means of a rearview mirror.

Transcranial Magnetic Stimulation

Participants wore a tightly fitting bathing cap on which the scalp positions for stimulation were marked. Motor-evoked potentials (MEPs) were recorded from the first dorsal interosseous (FDI) muscle of the dominant right hand. Surface Ag/AgCl electrodes were placed in a belly-tendon montage with the active electrode placed over the motor joint and the reference electrodes placed over the interphalangeal joint. Responses were amplified at a gain of 1000× by a Digitimer D360 amplifier (Digitimer, Hertfordshire, England), band-pass filtered (20 Hz – 2.5 kHz), and digitized by means of a CED Power 1401 controlled with Spike 2 software (Cambridge Electronic Design, Cambridge, England). The resting motor threshold (rMT), defined as the lowest stimulus intensity able to evoke five out of

ten MEPs with an amplitude of at least 50 μV, was determined by holding the stimulation coil over the optimal scalp position (i.e., the left motor cortex area producing the largest MEPs) for the right FDI muscle.

Stimulation sites were identified on each observer's scalp with SofTactic Navigator system (EMS, Bologna, Italy). Skull landmarks (nasion, inion, and two preauricular points) and about 60 points providing a uniform representation of the scalp were digitized by means of a Fastrak Polhemus digitizer (Polhemus, Colchester, VT). Coordinates in Talairach space [42] were automatically estimated by the SofTactic Navigator from an MRI-constructed stereotaxic template. The scalp location that corresponded best to the EBA coordinates [1] was identified and marked with a pen. Moreover, an occipital site corresponding to V1, 2 cm above and 2 cm lateral to the inion on the right, was targeted in order to control for nonspecific effects of rTMS on visual perception.

rTMS was performed by connecting two Magstim Model 200 stimulators with a Bistim module (The Magstim Company, Carmarthen-shire, Wales), producing a maximum output of 1.75 T at the coil surface (stimulus attenuation, 22%; duration, 1 ms; rise time, 110 μs). Two pulses were applied with an interstimulus interval of 100 ms by means of a 70 mm figure eight stimulation coil (Magstim polyurethane-coated coil). In keeping with the estimated timing of the TMS suppressive effect on extrastriate areas [19], the first pulse was delivered 150 ms after the onset of sample presentation; at this time interval, the stimulation of V1 is generally ineffective on visual tasks [19]. Stimulation intensity was 120% of the rMT for both pulses and ranged from 36% to 58% (mean = 47.9%) of the maximum stimulator output. For magnetic stimulation, the coil was held tangential to the scalp, with the handle pointing backward and laterally at a 45° angle from the mid-sagittal axis of the subject's head. For sham stimulation, the coil was oriented perpendicular to the scalp, with the border of one wing placed against the subject's scalp. This ensured that no magnetic stimulation reached the brain during sham stimulation and controlled for noise and the sensation of the coil against the head. The same stimulation intensity and timing were used for magnetic and sham stimulation. The coil was held by hand, and its position with respect to the marks was checked continuously. During sham and magnetic stimulation, participants wore commercial earplugs to protect their hearing. None of the subjects reported phosphenes after rTMS of V1 or EBA.

Procedure

Each subject was tested in one experimental session lasting approximately 2 hr. Participants completed a block of 32 practice trials, followed immediately by the experimental blocks. Each stimulus set was presented separately with a block design, and a Latin square balancing of the category order was used. A short rest was allowed before proceeding to a different stimulus category. For each category, two blocks of eight trials were presented in the EBA and V1 magnetic stimulation condition as well as in the sham stimulation condition. For each participant, each of the three stimulation conditions was repeated twice in a variable sequence that was counter-balanced across participants.

A trial started with the presentation of a central fixation point (lasting 500 ms) aimed at minimizing eye movements. Then, the sample stimulus was presented for 150 ms at the center of the monitor. Image persistence was limited by presenting a random-dot mask (9.1° × 9.1° in size) for 500 ms. This was obtained by scrambling the corresponding sample stimulus by means of custom-made image segmentation software. Immediately after the disappearance of the mask, the two probe stimuli appeared and remained on the screen until a response was made. Participants were asked to respond as quickly as possible by using their index or middle finger to press the left or the right key, respectively, on a custom-made response box. Each key corresponded to one of the two locations on the screen on which the probe stimuli were presented; the position of the probe stimuli was randomized in each trial. All participants used their right hand. RTs and accuracy were recorded and stored for automatic analysis.

Data Handling

Individual mean percentages of correct responses and RTs for each stimulus category were separately calculated in the EBA, V1, and

sham stimulation condition (16 trials per cell). Only RTs for correct trials were considered; moreover, RTs that fell below or above three standard deviations from each individual mean were identified for each cell and removed as outliers (2.2% of the total).

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