Extrastriate body area in human occipital cortex responds to the performance of motor actions

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A region in human lateral occipital cortex (the 'extrastriate body area' or EBA) has been implicated in the perception of body parts. Here we report functional magnetic resonance imaging (fMRI) evidence that the EBA is strongly modulated by limb (arm, foot) movements to a visual target stimulus, even in the absence of visual feedback from the movement. Therefore, the EBA responds not only during the perception of other people's body parts, but also during goal-directed movements of the observer's body parts. In addition, both limb movements and saccades to a detected stimulus produced stronger signals than stimulus detection without motor movements ('covert detection') in the calcarine sulcus and lingual gyrus. These motor-related modulations cannot be explained by simple visual or attentional factors related to the target stimulus, and suggest a potentially widespread influence of actions on visual cortex.

Neural activity in visual cortex can be modulated by many factors in addition to retinal stimulation, including attention, working memory, familiarity and integration of stimuli from different sensory modalities[1–4]. Eye movements also modulate the responses of cells in V1 and V4 to visual stimuli[5–8]. There is no evidence to date, however, of modulation of visual cortex by limb movements. Here we report modulations in lateral and medial occipital cortex while observers pointed with their hand or foot to visual targets. These modulations were observed after controlling for attention and sensory factors related to the stimulus, and even when the limb was not visible to the observer. The activated area in lateral cortex corresponded to the EBA, which responds selectively to images of human bodies or body parts[9,10]. Previous studies[9] have put forth the hypothesis that the EBA may be responsible for the identification of other people's bodies, inferring the actions of others, or perceiving the position of one's own body during the guidance of action. Our results suggest that this region, in addition to being activated by visual images of other people's body parts, is also modulated by planning, executing and imagining movements of the observer's hand or foot.

RESULTS

EBA is active for limb movements

We first tested the hypothesis that the EBA responds not only during the perception of body parts, but also during the execution of visually guided hand movements, and that its response is specific for hand movements as compared to eye movements or covert target detection. In the first experiment, subjects ($n = 15$) were directed to one of two peripheral visual locations by a central arrow cue. After a variable delay of 5–6 s, an asterisk was flashed for 100 ms at the location indicated by the cue (73% of trials) or at the opposite location. In different scans, subjects did one of three tasks. In the 'attention' condition, subjects covertly directed attention to the cued location (that is, they attended to the cued location while maintaining central fixation) and then covertly detected the target (that is, no motor response was made). In the 'saccade' condition, they prepared an eye movement to the cued location, followed by a saccade to the target location upon target presentation. And in the 'pointing' condition, they prepared to point with their right index finger at the cued location, followed by a pointing movement in the direction of the target upon target presentation. Maintenance of fixation during the attention and pointing conditions and during the cue period of the saccade condition was verified by eye movement monitoring. None of the presented results can be explained by a loss of fixation or the presence of head movements during pointing (**Supplementary Methods** online). Event-related fMRI methods were used to separate blood oxygenation level–dependent (BOLD) signals for the cue and target/response period.

The BOLD signal in lateral occipital cortex during the response to the target stimulus differed significantly across conditions (**Fig. 1a**). A region ($x, y, z = -46, -68, 4$) in the middle occipital gyrus, near/at the coordinates previously published for the EBA[9], responded more strongly in the Pointing condition than in either the Saccade ($P < 0.0001$) or Attention ($P < 0.0001$) conditions. Similar results were obtained for the right hemisphere ($x, y, z = 46, -62, 3$; **Supplementary Table 1** online).

Given that in all conditions the target was attended and detected, it seems unlikely that the enhancement for hand pointing reflected an attentional enhancement of the visual response to the target. However, the larger signal in the Pointing condition might have reflected a difference in visual stimulation produced by partial vision of the moving hand. Furthermore, the claim that this modulation occurred in the EBA was based on a comparison of atlas coordinates across experiments.

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Therefore, we conducted a second experiment ($n = 10$) in which vision of the body and hand was occluded. We also localized the EBA region within each subject using stimuli and a block paradigm that have been previously described[9], wherein pictures of body parts were alternated with pictures of object parts. In the main experiment, subjects performed the Attention and Pointing tasks of experiment 1, as well as a third task in which they pointed with their right foot. This latter condition was included to test whether the response in the EBA was hand-specific or could be induced by movements of other body parts. The positions of the hand and foot were monitored with a digital camera, and eye movements were also monitored.

The BOLD response in several regions of lateral occipital cortex was stronger during the perception of body parts than object parts (**Fig. 1b**). There were two distinct peaks of activation in the left hemisphere: a dorso-anterior peak ($x, y, z = –40, –58, 7$) and a ventro-posterior peak ($x, y, z = –48, –69, 6$). The ventro-posterior peak was closer to the EBA coordinates[9] ($x, y, z = –51, –72, 8$, shown as a blue square in **Fig. 1b**) than was the dorsal peak. Right-hand pointing produced a significantly stronger response in the ventral region than both right-foot pointing ($P = 0.014$) and attention ($P = 0.032$) whereas the response for right-foot pointing was stronger than for attention ($P = 0.0075$). The left dorso-anterior region did not show a significant difference across the three conditions. A similar trend was observed in the right hemisphere (**Supplementary Table 2** online).

There was considerable overlap between the voxels activated by the EBA localizer and those voxels activated by hand or foot pointing, although the latter two conditions were not clearly distinguished within the EBA (**Fig. 1c**). These results show that visually guided hand and foot movements activate lateral occipital cortex, largely within or near the EBA, in the absence of visual input from the moving limb. These modulations cannot be explained by simple sensory or attentional factors related to the target flash and detection, since these factors were also present in the covert attention task (experiments 1 and 2) and in the eye movement task (experiment 1).

To determine whether activation in the EBA was affected by vision of the hand, we compared the magnitude of the EBA activations in experiments 1 and 2. Spherical regions of interest (ROIs) with a diameter of 1 cm were centered on the EBA coordinates (from ref. 9). In the left EBA, the signal magnitude for right-hand pointing was significantly larger in experiment 1 than experiment 2 (time × experiment, $P = 0.036$), and no difference was observed in the attention condition ($P = 0.91$; **Fig. 1d**). A similar trend was observed in the right hemisphere, but the difference in the hand condition was not significant ($P = 0.06$). We also found that within both the left and right ROIs, the BOLD signal magnitude in experiment 2 was larger during the perception of body parts than object parts (left, $P = 0.000051$; right, $P = 0.0021$), confirming that these ROIs included the EBA. These
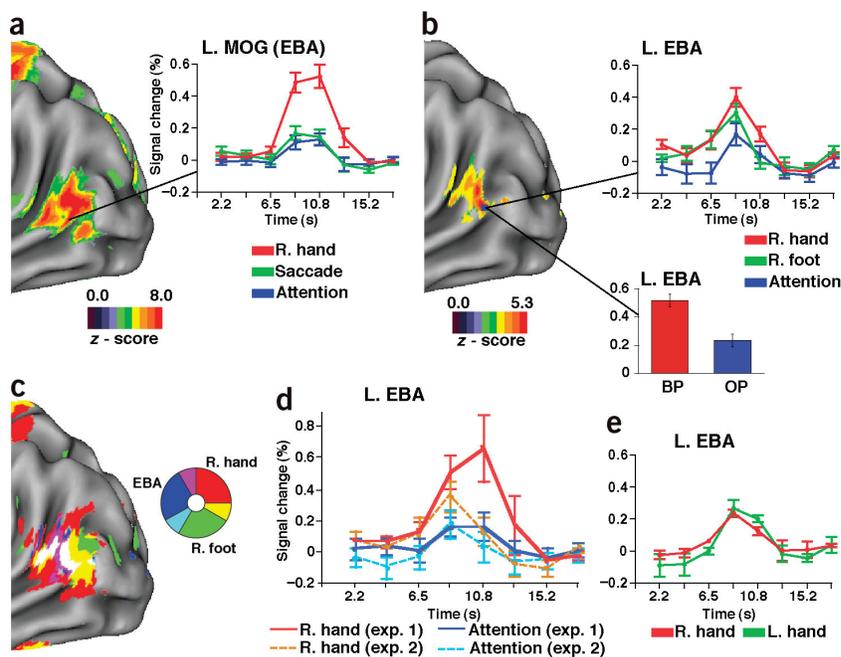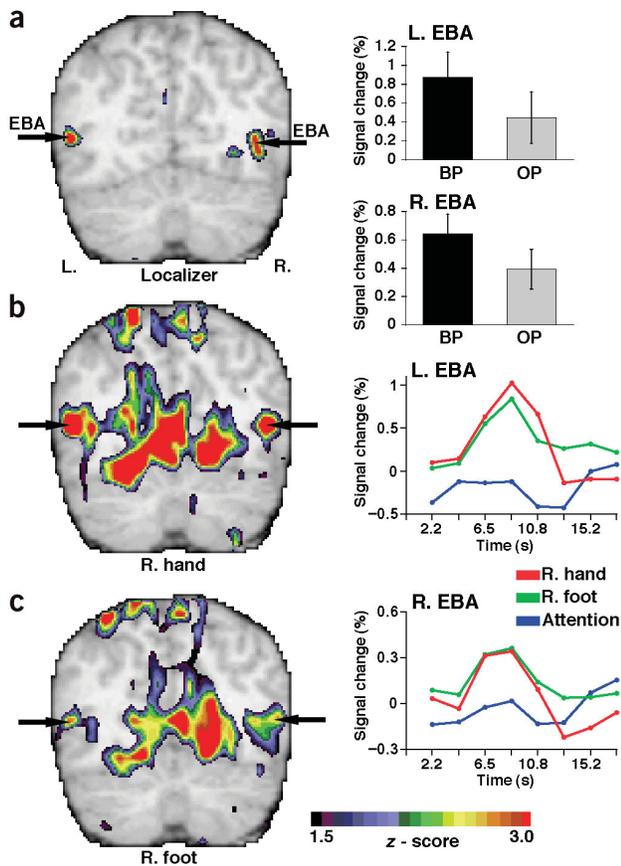

Figure 1 Group-averaged movement-related BOLD responses in the EBA. Lateral view of the left occipital lobe. (**a**) Group statistical map showing significant differences between the right hand pointing, saccade and attention tasks during the target period (valid trials only; experiment 1). The graph shows the group-averaged BOLD time course in the middle occipital gyrus (MOG) near/at the EBA, averaged over target direction. (**b**) Group statistical map from the EBA localizer scans showing the difference between body parts (BP) and object parts (OP), as well as the relative signal change compared to fixation for each condition. The position of the EBA[9] is shown as a blue square. The group-averaged BOLD response from the EBA for right hand pointing, right foot pointing and covert attention (experiment 2) are also presented. (**c**) Group statistical map of areas active during the right hand (red) and foot (green) pointing conditions of experiment 2. Significant voxels from the EBA localizer scans are shown in blue. White voxels indicate region of overlap between hand, foot and EBA localizer. (**d**) The group-averaged signal time course from the published EBA coordinates[9] during right hand pointing, with visual feedback of the moving hand (experiment 1) and without visual feedback (experiment 2). (**e**) The group-averaged time course in the left EBA during the right and left hand pointing tasks (experiment 3). L = left, R. hand = right hand pointing, R. foot = right foot pointing, L. hand = left hand pointing. Error bars represent the standard error of the mean (s.e.m.).

results suggest that the EBA is incrementally modulated by different kinds of signals, although they will need to be confirmed within the same experiment. Weak responses were elicited by visual attention, covert detection and saccadic eye movements; intermediate responses were obtained by pointing movements in the absence of visual input, and the largest responses were obtained when partial vision of the movement was allowed.

A third group of volunteers ($n = 5$) was tested to determine if EBA activity during pointing was modulated by the hand used to make the response. Subjects pointed to visual targets using either their left or right hand in different scans. Vision of the hand and body was occluded, eye movements were monitored, and the EBA was localized in each subject as in experiment 2. Both right and left hand pointing significantly activated the left EBA ($x, y, z = –45, –65, 12$; main effect of magnetic resonance frame, $P < 0.0001$ for right hand and $P < 0.0001$ for left hand), but showed no significant differences (**Fig. 1e**). Similar results were obtained in the right EBA ($x, y, z = 42, –58, 13$; **Supplementary Table 3** online).

EBA modulations from limb movements were readily observable in single subjects (**Fig. 2a–c**). The time courses confirm that responses were larger for the hand and foot conditions than for the attention condition (**Fig. 2**).

Figure 2 Movement-related BOLD responses in the EBA from a single subject (experiment 2). BOLD responses are superimposed on a coronal slice ($y = -69$). All statistical maps are z maps for contrasts based on an assumed hemodynamic response function. (**a**) Localization of the left and right EBA, and percent signal change for passive observation of body parts (BP) or object parts (OP) with respect to fixation. (**b**) Statistical map for right hand pointing task. Note the activity in the EBA and medial occipital cortex. (**c**) Statistical map for right foot pointing task. Signal time courses, averaged over target direction, are shown for the left and right EBA regions defined in **a**. Error bars represent the standard error of estimate (s.e.e.)[45].
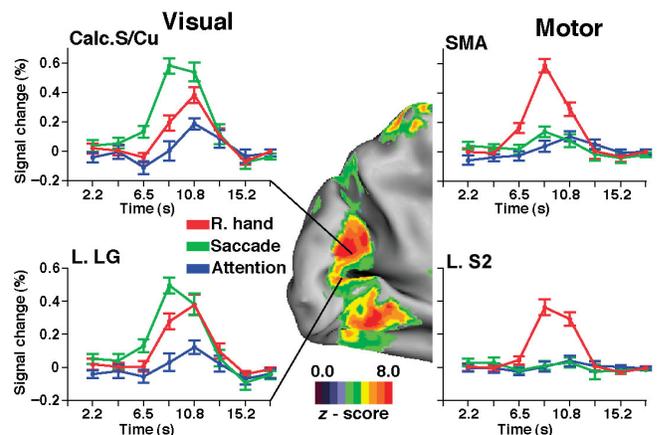
occipital cortex, including the calcarine sulcus (x, y, $z = 0$, -83, 10) and left (x, y, $z = -8$, -72, 1) and right (x, y, $z = 10$, -78, 0) lingual gyrus (**Supplementary Fig. 1** online). Activations were significantly larger for both hand pointing ($P < 0.0001$ in calcarine sulcus, $P < 0.0001$ in left lingual gyrus, $P < 0.0001$ in right lingual gyrus) and foot pointing ($P < 0.0003$ in calcarine sulcus, $P < 0.0003$ in left lingual gyrus, $P = 0.001$ in right lingual gyrus) than for Attention. Finally, no significant differences were observed between hand and foot pointing (experiment 2; **Supplementary Table 2** online), or between left hand and right hand pointing (experiment 3; **Supplementary Table 3** online).

EBA is active for motor imagery

A reviewer suggested that mental imagery of the movement might have activated visual cortex, as activity in some visual category-specific regions is increased by mental imagery of the preferred stimulus category[13]. Moreover, imagined movements and actual movements activate similar regions[14,15]. A block-design experiment was conducted in which three subjects performed the pointing task, eye-movement task, or a third task in which pointing movements were imagined. Although mental imagery activated the EBA, some EBA voxels responded more strongly during pointing than during either imagery or eye movements (see **Fig. 4** for data from a single subject; data for the remaining subjects are presented in **Supplementary Fig. 2** online). Imagery activated almost all classical motor areas (S2, SMA, premotor cortex, posterior parietal cortex, cerebellum), except S1/M1 (not shown), in good correspondence with previous studies[14,15]. Interestingly, whereas motor imagery activated some parts of the EBA, it did not activate medial visual cortex (calcarine sulcus and lingual gyrus).

Attention cannot explain motor-related activity

Another possible concern is that the attention task was not as demanding as the pointing or eye movement tasks, resulting in weaker responses in the covert attention condition. Two results

Medial occipital cortex is active for eye and limb movements

We also determined whether other visual regions were activated during limb movements (**Fig. 3**). Both the calcarine sulcus and bilateral lingual gyrus were significantly more activated during right-hand pointing than during attention ($P = 0.009$ for calcarine sulcus, $P = 0.0005$ for left lingual gyrus, $P = 0.0008$ for right lingual gyrus) and showed a stronger response in the Saccade condition than in the Pointing condition ($P < 0.0001$ for calcarine sulcus, $P = 0.0003$ for left lingual gyrus, $P < 0.0001$ for right lingual gyrus) and the Attention condition ($P < 0.0001$ for calcarine sulcus, $P < 0.0001$ for left lingual gyrus, $P < 0.0001$ for right lingual gyrus). See **Supplementary Table 1** online. The stronger responses in calcarine sulcus and lingual gyrus during saccades than during pointing may reflect shifts of the retinal image during eye movements and/or a spatially selective visual enhancement unique to eye movements[5,11,12]. As expected, limb movements strongly activated motor areas, including contralateral primary motor cortex, bilateral secondary somatosensory (S2) cortex and supplementary motor area (SMA). The time courses indicate that the latency of the activations in sensorimotor areas roughly matched those in visual cortex (**Fig. 3**).

Similar modulations in experiment 2, in which vision of the limb was occluded, were observed for both hand and foot movements in medial

Figure 3 Group-averaged movement-related BOLD responses in medial occipital cortex. The statistical map shows the significant differences between right hand pointing, saccade and attention conditions (experiment 1). The graphs show the group-averaged BOLD time courses, averaged over target direction (see **Fig. 1** legend), from visual and motor regions active in the statistical map. L = left, Calc. S = calcarine sulcus, LG = lingual gyrus, Cu = cuneus. SMA = supplementary motor area, S2 = secondary somatosensory area. Error bars represent s.e.m.

strongly argue against this hypothesis. First, the BOLD response in left EBA was significantly higher ($P = 0.00016$) during the preparation of a pointing movement than an eye movement, but there was no significant difference between the preparation of an attention shift as compared to both a pointing movement and an eye movement. A similar trend was observed in the right hemisphere, but the difference between conditions was not significant. These data suggest that the attentional load was similar during the preparation of hand movements and covert spatial attention shifts to a target location (**Supplementary Fig. 3** online, panel a).

Second, the right temporal-parietal junction (TPJ) is thought to be involved in the reorienting of attention to unexpected events[16], as it responds more strongly to visual stimuli presented at unattended than attended locations. In experiment 2, the BOLD signal during each task (Attention, right hand Pointing, right foot Pointing) in right TPJ (x, y, $z = 56$, -43, 6) was also significantly larger during invalid trials (*i.e.*, when the target was presented at an unattended location (see Methods) than during valid trials (*i.e.* when the target was presented at the attended location; $P < 0.04$). Notably, the difference in the amplitude of the response for invalid and valid trials was similar across conditions. Therefore, reorienting of attention to an unexpected target produced equivalent responses in the three conditions. Moreover, there was no difference in the amplitude of the response in right TPJ for arm movements and covert detection, which suggests that both tasks were equally difficult. Covert detection produced a non-significant trend for stronger responses than did foot movements (**Supplementary Fig. 3** online, panel b). Therefore, we conclude that the covert attention task used in this study was effective, and that the attentional load was not higher during limb movements both during preparation (cue period) and target detection/response execution (test period).

Both the EBA and some regions in medial visual cortex responded more strongly during pointing than during covert detection (Attention), but they were distinguished by differential activation during eye movements, imagined limb movements and planning. Medial visual regions responded more strongly during saccades than during pointing, whereas the EBA responded more strongly during pointing, with little response to saccades. Moreover, the EBA was recruited by imagining and planning of pointing movements, whereas medial visual cortex showed no response to either motor imagery or planning.

DISCUSSION

Until now, the EBA has been considered a high-level, category-specific object recognition area that is specialized for the analysis of human bodies[17], similar to category-specific areas in visual cortex for faces and places. Category-specific processing modules are thought to comprise initial cores of knowledge around which human language is organized during child development[18].

Our results indicate that in addition to this visual recognition function, the EBA integrates visual, spatial attention, and sensory-
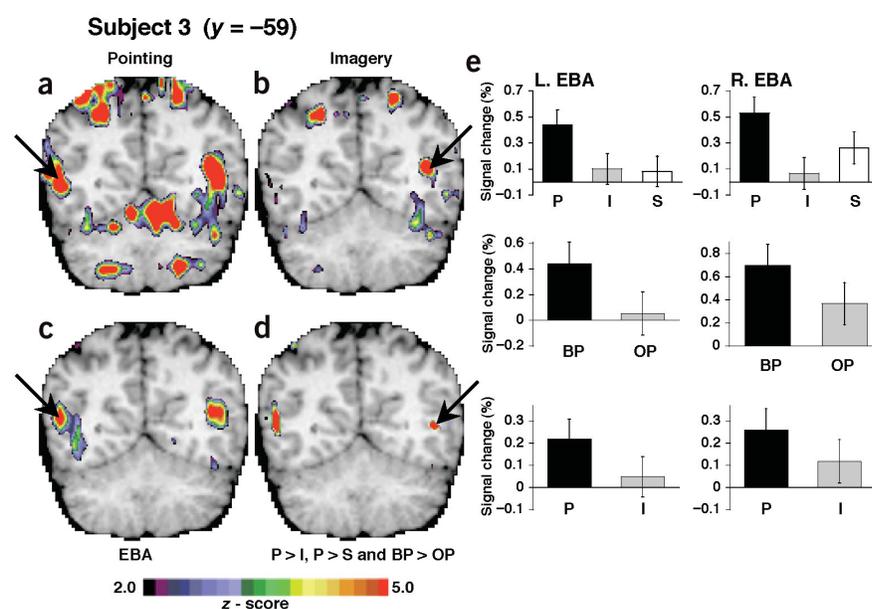

Subject 3 ($y = -59$)

Figure 4 BOLD responses in the EBA from a single subject during the pointing and imagery conditions. Significant BOLD responses are superimposed on a coronal slice ($y = -59$). (**a**) Pointing with the right hand, no visual feedback; (**b**) imagining pointing with the right hand; (**c**) EBA localizer, observation of body parts vs. object parts; (**d**) EBA voxels with significantly greater activity during pointing than imagery and saccades. (**e**) Top row: the percent signal change for pointing (P), imagery (I) and saccade (S) tasks as compared to fixation baseline, in the left and right EBA from the voxels in **d**. Middle row: percent signal change to body parts (BP) and object parts (OP) versus fixation baseline from the same voxels in panel **d**. Bottom row: percent signal change for pointing (P) and Imagery (I) tasks versus fixation baseline for all significantly active voxels in the left and right EBA ($z \geq 2.6$, $P < 0.01$ uncorrected). Error bars represent s.e.e.

motor signals involved in the representation of the observer's body. A limb movement may affect the observer's body representation through proprioceptive inputs that result from the movement. Although to our knowledge there have not been reports of proprioceptive activation of lateral occipital cortex or other regions in the occipital lobe, there have been reports that activity in visual cortex can be modulated by tactile information. Both congenitally and late-onset blind subjects show strong activation in visual cortex (V1, V2, VP, V4v and LOC (lateral occipital complex)) during Braille reading, which requires a mapping of tactile symbols onto the language system[19]. The LOC is modulated not only during visual object recognition, but also during the recognition of haptic objects[20]. Finally, a tactile stimulus may increase the visual response to a visual stimulus when both are presented simultaneously at the same spatial location[4].

A limb movement may also affect a body representation through a corollary discharge signal, which is used to adjust for changes in sensory input caused by the movement[21–23]. This motor-generated signal may activate the EBA and dynamically update a body representation. Similar mechanisms have been discovered in the superior colliculus, posterior parietal cortex and in several visual areas during saccadic eye movements for the updating of retinotopic representations[23–25]. Interestingly, there is evidence that areas in lateral posterior cortex near the EBA are involved in the representation of the body schema. A recent study demonstrated that an illusory perception of body movement can be induced by electrical stimulation of a region near the EBA in the angular gyrus[26]. Lesions in the angular gyrus and lateral occipital cortex, particularly in the left hemisphere, induce disturbance and misperception of the body schema[27,28].

If the EBA is involved in representing the observer's body, it is necessary to explain how a body map contributes to the perception of another person's body. Similarly, if the EBA is only involved in the perception of the bodies of other people, it is necessary to explain how movement of the observer's body can affect how other bodies are perceived.

One possibility is that the EBA is part of a system for both perception and action, similar to more anterior areas in the superior temporal sulcus (STS)[29]. Human and macaque STS contains neurons that respond to the observation of biological actions such as grasping, looking or walking[30,31]. The STS is also part of the so-called mirror neuron system, along with inferior frontal cortex (area F5 in macaque) and the anterior parietal cortex (area PF in macaque)[32–34]. This is an ensemble of areas in which neurons respond to the observation of actions performed by other people, as well as to the execution/imitation of the same actions performed by the observer (at least F5 and PF). It has been proposed that the mirror neuron system may mediate the understanding of actions through a mechanism by which motor representations 'resonate' to the observation of other people's actions. That is, the automatic recruitment of motor representations by visual information would allow the observer to 'match' and thus understand the action of others (the direct-matching hypothesis).

We do not know if the EBA is a 'mirror neuron' area, although some of its physiological properties suggest it might be. The EBA responds more strongly to moving than static human forms (and objects), especially when the motion is natural[9]. This is analogous to the response of neurons in human and macaque STS. Our results show that this area is modulated when the observer makes goal-oriented actions toward targets. These features are also similar to those reported in mirror neurons in areas F5 and PF. It will be interesting to test the activity in the EBA using protocols in which observation and execution/imitation of actions are directly compared[29].

Although action-related modulation of visual cortex was not unique to the EBA, it was not present in many visual areas. We compared attention-, saccade- and pointing-related responses in functional regions selected from the literature (fusiform face area (FFA), parahippocampal place area (PPA), LOC, middle temporal area (MT) and superior temporal sulcus (STS); **Supplementary Table 4** online). Modulations by limb movements did not occur in FFA, PPA or anterior STS, but did occur in MT and LOC in foci localized within 1 cm of the center of the EBA. Given that functional areas MT and LOC share roughly 30% of voxels with the EBA, even within a single subject[9], it was not surprising to find action-related modulations in these adjacent regions. Detailed single-subject studies will be necessary, however, to determine whether action-related signals are limited to EBA or also involve adjacent functional regions.

The additional observation that medial occipital cortex, near or at V1/V2, is more strongly activated by visually guided eye movements and limb movements than by covert detection indicates that action-related modulations can occur in visual regions other than the EBA. Anatomically, areas V1/V2 may receive tactile feedback through area V6, which has reciprocal connections to both retinotopic visual areas (V1/V2/V3) and bimodal visual-tactile areas (V6a/MIP/VIP)[35]. Accordingly, we recently reported hand-specific planning and execution signals in various posterior parietal regions including the superior parietal lobule and precuneus, which map onto macaque areas MIP and PIP based on multidimensional warping of human and macaque brains[36]. Additional multimodal input into peripheral V1 might come from auditory cortex as well as from the superior tempo-ral polysensory area (area STP), which contains visual, auditory and tactile unimodal and multimodal neurons[37,38].

In conclusion, while explorations of the function of action-related activations in visual cortex are at an early stage, the results reported here indicate that these modulations are present in several different regions.

METHODS

Subjects. Fifteen subjects (6 females; age 19–24 years, mean 22) were recruited from the Washington University community for experiment 1. Ten subjects (8 females, age 19–25, mean 21.7) participated in experiment 2, five subjects (3 females; age 19–25, mean 21) in experiment 3 and three subjects (2 females; age 18–26, mean 22) in experiment 4. All subjects were strongly right-handed as measured by the Edinburgh Handedness Inventory, had normal or corrected-to-normal vision, and a normal neurological history. Informed written consent was obtained in accordance with procedures approved by the human studies committee at Washington University School of Medicine.

Apparatus. For a detailed description, see **Supplementary Methods** online.

Task and procedures. A fixation cross-hair was displayed inside a gray diamond (size 1.6°) on a black background at all times during experiments 1–3. A change in the color of the fixation point from red to green indicated the start of a trial. Simultaneously, one side of the diamond was illuminated for 100 ms, indicating either a left or right location (cue stimulus). After a random delay (4.76–5.86 s in experiment 1 and 2.6–3.7 s in experiments 2 and 3), a white asterisk (target stimulus) was flashed for 100 ms 7.3° to the left or right of fixation. The stimulus occurred at the cued location (valid trial) on 73% of trials (75% in experiments 2 and 3), and at the opposite location (invalid trial) on 27% (25% in experiments 2 and 3) of the trials. In the attention condition, a random digit (1–9) was occasionally presented (either 0, 1 or 2 times in a block of trials) instead of the asterisk (only in experiment 1). After another interval (0.44–1.54 s), which yielded a fixed trial (cue + test) duration of 6.50 s (4.33 s in experiments 2 and 3), the fixation point changed color from green to red to indicate the end of the trial. Trials were separated by a random intertrial interval (ITI) of 2.16–6.50 s, in which the fixation point remained red. On 21% (20% in experiments 2 and 3) of the trials, only the cue stimulus was presented, followed by a fixed interval of 4.23 s (2.07 s in experiments 2 and 3) before the start of the ITI. The presentation of cue-only trials was necessary to separate cue and target fMRI responses within a trial without assuming a hemodynamic response function[39–41].

In experiment 1, three different tasks were performed. In the right-hand pointing task, subjects used the cue to prepare a pointing movement to the left or right with their right index finger. After the target was flashed, subjects pointed as quickly as possible in the direction of the target location (without touching the screen), and then returned to the starting position. Some subjects, because of their body size, could see their finger during the execution of the pointing movement (see **Supplementary Methods** online for additional details).

In the saccade task, the cue was used to prepare a saccadic eye movement to the left or right. After the target was flashed, subjects looked at its location, and then quickly looked back at the fixation point. In the attention task, subjects covertly shifted and maintained attention at the cued location, and returned attention to the center after the presentation of the target. Subjects reported whether and how many times (0, 1 or 2 times) a random digit was presented in the course of a block of trials. This secondary task insured that subjects attended to the peripheral target on each trial. Mean accuracy was 97% correct. For each subject, there were 15 scans (5 scans per task) and each scan/block involved 28 trials.

In experiment 2, three different tasks were performed: right hand pointing, attention and right foot pointing. The right hand pointing task was the same as in experiment 1. The attention task was similar to the task in experiment 1, except that no digits were presented. The right foot pointing task was similar to the right hand pointing task, but subjects pointed with their right foot instead of their right hand. Each subject (n = 10) performed 15 scans, 5 scans per task, and each scan consisted of 30 trials (see **Supplementary Methods** online for additional details).

In experiment 3, only the pointing task was used. In different blocks/scans, subjects ($n = 5$) used either their left or right hand. Each subject performed 14 scans, 7 scans per task, and each scan consisted of 30 trials.

Experiment 4 involved a block design. Subjects performed four tasks: fixation, saccadic eye movements (saccade), right hand pointing movements (pointing), and mental imagery of pointing movements (imagery) to visual targets. In the imagery condition, subjects were asked to imagine their hand moving the same way it moved during the right hand pointing task, but without making any movement and keeping their hands relaxed (see **Supplementary Methods** online for additional details).

In experiments 2, 3 and 4, vision of the hand and foot was occluded by a modification to the periscopic mirror. In experiments 2 and 3, a video camera was used to monitor the position of the hand and leg to confirm that movement had occurred only during the target period.

In experiments 2, 3 and 4, all subjects performed an additional session to localize the EBA. We used a protocol similar to a previously published study[9]. Grayscale photographs of human body parts and object parts on a uniform background (provided by the authors of ref. 9) were presented in separate blocks within a scan (for details, see **Supplementary Methods** online). Each subject received 3 or 4 scans. Subjects were asked to pay attention to the pictures and to make no response.

fMRI scan acquisition and data analysis. A Siemens whole body 1.5 T Vision MRI scanner (Siemens AG) and an asymmetric spin-echo, echo-planar sequence were used to measure blood oxygenation level–dependent (BOLD) contrast over the whole brain (T$R = 2.165$ s, TE $= 37$ ms, flip angle $= 90°$, 16 contiguous 8 mm axial slices, 3.75×3.75 mm in-plane resolution). Anatomical images were acquired using a sagittal MP-RAGE sequence (T$R = 97$ ms, TE $= 4$ ms, flip angle $= 12°$, inversion time T1 $= 300$ ms). Functional data were realigned within and across runs to correct for head motion using six-parameter rigid-body realignment.

In each subject, hemodynamic responses were estimated without any shape assumption at the voxel level using the general linear model. Random-effects analyses were performed by entering the individual time points of each estimated hemodynamic response into voxel-level and regional ANOVAs. In experiment 1, ANOVAs were run on the time courses from the target period with the following factors: MR frame (1–8), task (right hand pointing, saccade, attention), target visual field (left, right) and target validity (valid, invalid). These analyses were based on about 2,100 trials per task over the 15 subjects. Experiment 2 was analyzed in a similar fashion, with three levels on the Task factor (right hand pointing, right foot pointing, attention). Analyses were based on about 1,500 trials per task over the 10 subjects. In experiment 3, the factor Task included only two levels (right hand pointing, left hand pointing) and the analyses were based on about 1.050 trials per task over the 5 subjects. For the analysis of the EBA localizer scans, the only factor was task (viewing pictures of body parts versus viewing object parts).

Experiment 4 was analyzed as a block design experiment. Single-subject z maps of contrasts (pointing minus imagery, pointing minus saccades, perception of body parts minus perception of object parts, pointing minus fixation, imagery minus fixation) were first thresholded at $z = 2$ ($P < 0.05$ uncorrected). Next we found the overlap between the images for pointing minus saccades and perception of body parts minus perception of object parts to create a mask that was applied to the pointing minus imagery map.

Group-average ANOVA F maps were transformed to z maps, corrected for multiple-comparison and adjusted for correlations across timepoints by using previously published methods[42]. The coordinates of responses in z maps were identified by an automated algorithm that searched for local maxima and minima, and localized according to a stereotactic atlas[43]. Group-average z maps were projected on the Colin-brain atlas[44].

Note: Supplementary information is available on the Nature Neuroscience website.

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