Whose arm is it anyway? An fMRI case study of supernumerary phantom limb

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Summary
Under normal circumstances, information from a number of sources is combined to compute a unitary percept of the body. However, after pathology these influences may be perceived simultaneously, resulting in multiple dissociated conscious representations. In a recent paper, we described subject E.P., a right-handed female stroke patient with a right frontomesial lesion who sporadically experiences a supernumerary ‘ghost’ left arm that occupies the previous position of the real left arm after a delay of 60–90 s. We used a delayed response paradigm with functional MRI to examine the haemodynamic correlates of E.P.’s illusion. Comparison of periods of time during scanning when the ghost arm was present against when it was not revealed a single cluster (9 voxels, \(t = 5.11, P < 0.012\) corrected for multiple comparisons) located on the right medial wall in the supplementary motor area (‘SMA proper’). Our results suggest that areas traditionally classified as part of the motor system can influence the conscious perception of the body. We propose that, as a consequence of her injury, E.P. is aware of the position of the phantom limb in this ‘action space’ while also continuing to be aware of the true position of her real limb on the basis of afferent somatosensory information.

Keywords: phantom limb; SMA; functional neuroimaging; event-related; action space

Abbreviations: fMRI = functional MRI; HRF = haemodynamic response function; M1 = primary motor cortex; SMA = supplementary motor area; VAC = vertical line through the anterior commissure; VPC = vertical line through the posterior commissure

Introduction
The aim of this study was to use functional MRI (fMRI) to investigate the haemodynamic correlates of supernumerary phantom limb in a single patient, E.P, who experiences a third, ‘ghost’ arm that mimics the previous position of her real left arm (Hari et al., 1998). We propose that this illusion arises from the influence of a previous state of the patient’s motor system on her current perception of limb position.

The term ‘body schema’ was introduced to neurology by Head and Holmes (1911), who were the first to systematically study patients’ perceptions of their bodies. They postulated that the spatial perception of one’s body is updated ‘on-line’ by successive changes in position. Spatial perceptual disorders could therefore arise from peripheral disruptions of incoming afferent information (traumatic deafferentation of a limb) or after damage to brain areas thought to be involved in the production of the body schema, e.g. the ‘neglect’ experienced after right parietal stroke (Vallar, 1997). There is thus a necessary interplay between ‘bottom-up’ (stimulus-driven, originating from the periphery) and ‘top-down’ (originating within the nervous system) influences on the body schema.

Experimental evidence now suggests that top-down influences need not originate from traditional sensory or association cortex areas (Jeannerod, 1994). For example, the concept of ‘efference copy’, as introduced by Helmholtz (Helmholtz, 1995), suggests that a copy of one’s intended movement is used every time a voluntary action is planned, such that the sensory consequences of the action can be cancelled (Blakemore et al., 1998). Most contemporary accounts of efference copy have claimed that it is unconscious, or acts to cancel percepts rather than generate them. Nevertheless, some clinical and experimental observations suggest that this information, in particular the state of the motor system, can influence subjective perception of the body. The information can take a number of different forms (Jeannerod, 1997), such as the initial spatial configuration of
the body before movement, the predicted goal of the movement, the sensory information generated by the movement (reafference), or the predicted sensory information (the consequences of the movement).

However, our daily sensation is typically of a unitary self rather than multiple separate ‘visual’, ‘proprioceptive’ or ‘motor’ selves. Some researchers have suggested that this is because sources of information from different modalities are combined in ‘higher’, multimodal areas, such as the premotor cortex (Graziano and Gross, 1998). While multiple sources of sensory information may be combined in this fashion, it is unlikely that all of the possible influences on the subjective perception of body position ultimately feed into a common location (Lackner and DiZio, 2000). It is therefore conceivable that, while under normal circumstances one or a combination of the above factors drives perception to produce a single percept of the body, after pathology these influences may be perceived simultaneously, resulting in multiple conscious representations of the same body part.

The subject E.P. allowed us to evaluate this question empirically. She experiences a supernumerary phantom limb or ‘ghost’ arm that occupies the previous position of her real left arm after a delay of 60–90 s, subsequent to a right frontomesial infarction impinging on medial wall structures, including the presupplementary motor area (pre-SMA) and cingulate motor areas (Fig. 1). Reports of supernumerary phantom limbs (e.g. Halligan et al., 1993, 1995) are rarer than published reports of phantom limbs occurring after amputation or brachial plexus avulsion, and the mechanisms underlying the generation of supernumerary phantoms are unknown. We used a combined event- and epoch-related design in fMRI to isolate the haemodynamic correlates of E.P.’s perception of her ghost arm.

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Material and methods

Patient details

Lesion and neurological examination

The subject’s neurological details have been reported previously (Hari et al., 1998). All clinical details were collected during previous investigations. The subject was a 42-year-old right-handed female native Finnish speaker with no previous psychiatric history. In January 1994, E.P. was admitted to hospital complaining of severe headache, left hemiparesis and acute global aphasia. Upon examination a subarachnoid haemorrhage and extensive oedema were found, caused by an aneurysm in the left pericallosal artery. Small resections of the right cingulate gyrus and anterior corpus callosum had to be made during surgery to deal with this.

After the operation the subject was tired and feverish and was slow to recover. Diagnosis of a right frontomesial infarction was confirmed after a CT scan in April 1994. A T1-weighted MRI acquired using a Siemens Magnetom Vision (Siemens, Erlangen, Germany) at 1.5 T clearly showed a wedge-shaped infarction in the subject’s right frontal gyrus. Neurological examination 36 months after the operation (January, 1997) showed a well-oriented subject. There were no cranial nerve abnormalities, muscular strength and tendon reflexes were symmetrically normal and the subject had a bilaterally negative Babinski reflex. Sensitivities to sharp pain and soft touch were slightly lower on the left than the right of the face and limbs. Vibration, thermal sensitivity and position senses were bilaterally normal. Discrimination of touch on the fingers did not differ substantially between the left and right sides. Tactile naming of objects resulted in 15 out of 15 correct responses with the right hand and 11 out of 15 correct responses on the left.

Immediately after the operation, the subject’s left hand displayed symptoms typical of callosal disconnection: intermanual conflict, a grasp reflex (grasping objects and not letting them go), the hand being described by the subject as having a ‘will of its own’. In addition, the subject experienced difficulty in tasks requiring bimanual coordination and showed motor perseveration with rhythmic move-
experience the phantom (D), she was instructed to move her left arm again (thus mimicking the motor response that ended the ‘phantom on’ period). This was repeated six times in each session.

Fig. 2 Schematic representation of two cycles of the experimental paradigm. Each timeline is a separate experimental condition. For analysis, the right button-press (timeline A) and left arm move conditions (timeline B) were each split into two regressors, depending on whether they had occurred in the context of a ‘phantom on’ or a ‘phantom off’ condition. Here they are each represented by a single timeline for the sake of clarity. The time at which each experimental condition occurred is indicated by an increase in height from the prestimulus baseline. E.P. indicated the presence of the phantom with a right index finger button-press (A), which was also the beginning of the ‘phantom on’ period (C). After a delay, during which E.P. perceived the phantom’s presence (C), E.P. was instructed to move her left arm (B), abolishing the phantom. After a delay of 10 s, E.P. was instructed to press the button box again (mimicking her motor response to signal ‘phantom on’), and after a delay during which E.P. did not experience the phantom (D), she was instructed to move her left arm again (thus mimicking the motor response that ended the ‘phantom on’ period). This was repeated six times in each session.

Body schema distortions
Roughly 3 weeks after her operation, E.P. reported distortions of her body schema which had begun immediately after her initial operation. E.P. frequently (i.e. several times a day) experienced a supernumerary, ‘ghost’ arm and less often a supernumerary leg. These extra limbs were always experienced on the left side of E.P.’s body: the arm typically appeared medial to the left shoulder and the leg appeared at the same place as the real left leg. The extra limbs did not replace E.P.’s perception of her real limbs: all three arms or legs were perceived simultaneously (but see below). These experiences have not diminished over time (the subject was scanned in June 1999).

Unlike many other published cases of supernumerary phantom sensations following central damage (Weinstein et al., 1954; Halligan et al., 1993; Sellal et al., 1996), E.P. is aware that her experiences are abnormal and stem from her neurological insult, and shows insight into her condition. There is no denial of the symptoms and no signs of neglect. If the phantom percept continues for long enough (over a period of tens of minutes), E.P. begins to perceive only the phantom arm or leg—her perception of her real limbs begins to fade. This illusory percept has persisted since E.P.’s infarct, while her other symptoms (e.g. intermanual conflict) have faded.

The percept is realistic enough to cause E.P. confusion: for example, when shopping after her operation she felt she had accidentally taken bags from other people, because the third arm made her feel as though she was carrying three bags. While this can cause her some embarrassment, E.P. has never attempted to rationalize or ignore the ghost’s presence. Perception of the ghost arm and leg are cancelled by vision of the normal left arm/leg. Continual tactile stimulation such as peripheral electrical stimulation to the left arm also prevents E.P. experiencing the ghost.

Experimental details
The Joint Medical Ethics committee of the National Hospital for Neurology and Neurosurgery and the Institute of Neurology, London, approved the study. The subject’s written informed consent was obtained before the experiment began. E.P. was familiarized with the behavioural paradigm (Fig. 2) outside the scanner. During scanning, E.P. lay supine on the scanner with her eyes closed and her arms by her sides. E.P. moved her left arm. After about 90 s, when E.P. sensed the presence of the phantom, she pressed a button with her right index finger (Fig. 2, first event in condition A). After a variable delay (between 21 and 23.5 s, mean 22.3 s) E.P. received an auditory command in Finnish to move her left arm (Fig. 2, first event in condition B), which caused the phantom perception to disappear. The period between E.P. signalling the presence of her phantom arm and moving her left arm was designated the ‘phantom on’ period (Fig. 2, condition C). During this period, E.P. consistently perceived her phantom left arm. This was confirmed by questioning E.P. after each scanning session.

After 10 s, the subject received a command to press the button box as before (second event, condition A), and after a further variable delay (as above) to move her left arm (second event, condition B). The period between E.P. pressing the button box and moving her arm was designated as the ‘phantom off’ period. The length of this period (between 21
and 23.5 s, similar to the length of the ‘phantom on’ condition) was chosen because, even though E.P. was lying at rest, this time is too brief for the phantom sensation to develop. The variable length of each ‘phantom on’ and ‘off’ period increased the effective sampling frequency of the haemodynamic response function (HRF) (Josephs et al., 1997). A complete cycle of the paradigm consisted of a ‘phantom on’ followed by a ‘phantom off’ period. Six cycles of the paradigm were repeated over each session.

**Scanning parameters**

Data were acquired from five experimental sessions; the data from Session 2 were not analysed as the subject dropped the button box. Because it took E.P.’s phantom arm a variable amount of time to be perceived, the length of each session differed (Session 1, 350 scans; Session 3, 300 scans; Session 4, 295 scans; Session 5, 315 scans). The first four scans of each session were removed prior to analysis to account for T1 equilibration effects. E.P. remained in the scanner bore between sessions, which were typically separated by a gap of 10 min.

The data were acquired on a Siemens Magnetom Vision scanner at 2 T. Each fMRI volume scan consisted of 48 transverse slices [in-plane matrix 64 × 64; voxel size 3 × 3 × 2.1 mm with a 1.05 mm gap between adjacent slices; TE (echo time) = 30 ms; TR (repetition time) = 2.83 s]. A T1-weighted MRI of the subject (TE = 4.1 ms; 1 × 1 × 1.5 mm) was acquired to facilitate anatomical localization of the functional data.

**Image preprocessing and analysis**

All data processing was carried out using SPM99 (Wellcome Department of Cognitive Neurology, London, UK). All functional volumes were realigned using the first volume from the first session as a reference (Friston et al., 1995). To correct for differences in slice acquisition times within each volume, each slice was interpolated in time to approximate a common acquisition time, using the middle slice as a reference. The data were resampled at 2 × 2 × 2 mm prior to smoothing with an 8 mm full width at half maximum Gaussian kernel. The subject’s T1 structural scan was coregistered to the mean functional volume by maximizing the mutual information between the two volumes (Collignon et al., 1995). The subject’s functional data were linearly normalized to a standard anatomical coordinate system. No non-linear spatial transformations were used.

Functional volumes from all sessions were treated as a time series and experimental effects estimated using a multisession design matrix that included separate session mean terms. Each session contained six experimental effects of interest modelled as ‘event’ or ‘tonic’ responses. The four events comprised E.P.’s right index button-presses and left arm movement conditions, separated into four conditions by their occurrence in the context of the ‘phantom on’ and ‘phantom off’ conditions. The expected haemodynamic response to each event was modelled by convolving delta functions that indexed each event with a synthetic HRF (Friston et al., 1994) and its first-order temporal derivative. The inclusion of the
temporal derivative has been shown to increase sensitivity in even-related analyses (Hopfinger et al., 2000).

The two tonic conditions encompassed the ‘phantom on’ and ‘phantom off’ responses. Each of these was modelled using a boxcar function convolved with a synthetic HRF. In addition to the six experimental effects, each single-session partition of the design matrix contained six covariates representing the estimated movement parameters for each scan (obtained from the realignment parameters). To remove low-frequency noise, the data were high-pass filtered using a set of discrete cosine basis functions with a cut-off period of 240 s. Temporal autocorrelation was dealt with using the method of Worsley and Friston (1995) by temporally smoothing the session time series with a Gaussian kernel of 3 s full width at half maximum.

Linear contrasts of the covariates were evaluated for the main effects of each event response and for the contrast ‘phantom on’ – ‘phantom off’. Results were displayed as a voxelwise statistical parametric map of t or F values. Voxels that survived a threshold of P < 0.05 corrected for multiple comparisons across the entire volume were reported as significant. A cluster threshold of three contiguous voxels (k = 3) was used.

Results
As the subject’s functional and structural data were not normalized to a standardized anatomical template (as defined by Talairach and Tournoux, 1988), all locations of activated voxels are discussed with reference to their anatomical location in E.P.’s brain.

Behavioural data
The length of time required before E.P. reported her perception of the phantom from rest (i.e. the time between cycles of the experiment) (Fig. 2) was variable (mean ± standard error of the mean: Session 1, 109.2 ± 20.8 s; Session

![Image](image_url)
Main effects of event conditions
We first examined simple movement-related responses from E.P.’s brain. The brain in Figure 3 contains voxels that exhibited statistically significant \( P < 0.05 \) corrected for multiple comparisons across the volume) increases in BOLD signal during E.P.’s right index finger presses across all four scanning sessions. Clusters can be seen in the left precentral gyrus (cluster size 354 voxels; \( F = 11.52 \)) and left medial wall (53 voxels; \( F = 7.97 \)). This pattern is similar to that of results from previous fMRI studies examining the neurovascular correlates of simple motor actions (e.g. Rao et al., 1993). The activated area of the left precentral gyrus corresponds to the ‘hand knob’ (Yousry et al., 1997) of the primary motor cortex (M1). The location of the medial wall cluster [the y coordinate in the space of Talairach and Tournoux (1988) of the peak voxel is \( -8 \)] is consistent with the location of the human SMA proper as posterior to the vertical line through the anterior commissure (VAC). We also observed activation to this contrast in the bilateral posterior parietal cortex and the right superior occipital cortex.

The graphs in Figure 3 represent the evoked activity at the peak voxel of the SMA and M1 clusters across each of the four simple movement conditions. Conditions A and C represent right button-presses and conditions B and D left arm movements. The voxels display different activity depending on movement type—significant responses to conditions A and C and non-significant responses to B and D. Although the evoked activity associated with these simple movements was not of prime interest in the study, they serve as an internal control of the validity of the BOLD measure as an indicator of neurovascular change in E.P.’s brain.

Contrast of tonic conditions: ‘phantom on’ – ‘phantom off’
The results of the ‘phantom on’ – ‘phantom off’ contrast are shown in Figure 4. Only the orthogonal components of both regressors (with respect to the rest of the experimental model) were tested. The contrast therefore identifies voxels where there is a statistically significant positive difference \( P < 0.05 \) corrected for multiple comparisons) between the parameter estimates of the ‘phantom on’ covariate and the ‘phantom off’ covariate after the variance explained by the remainder of the model has been accounted for.

Only a single cluster of activated voxels survived correction for multiple comparisons—a cluster on the right medial wall (cluster size 9 voxels, \( t = 5.11, P < 0.012 \)) that we identify as lying in the anterior part of the SMA proper. The fitted response and adjusted data, plotted as a function of peristimulus time for this peak voxel, are shown in the bottom half of Figure 4.

A number of progressively more detailed classification schemes have been applied to this portion of cortex. Brodmann originally defined this area as area 6 using cytoarchitectonic criteria, noting that it seemed to constitute a separate lateral and medial area. Early stimulation studies (Penfield and Welch, 1951; Woolsey et al., 1952) defined the region as a single area, as it contained a complete somatotopical map of body movements. It is now accepted that the SMA can be segregated anatomically and functionally into two separate areas according to definitions derived from comparative neuroanatomy (for review see Rizzolatti et al., 1998). In addition, most researchers agree in principle with the classification scheme of Picard and Strick (1996) for the medial wall, defining four areas: anterior SMA (pre-SMA), posterior SMA (SMA proper), rostral cingulate zone (RCZ) and caudal cingulate zone (CCZ). This demarcates the SMA and pre-SMA using the VAC line, perpendicular to a line drawn through the anterior and posterior commissures (AC–PC). After the brain has been spatially normalized into the space of Talairach and Tournoux (1988). While no non-linear transforms were applied to E.P.’s data, we transformed her brain linearly such that the VAC and VPC lines were comparable with those defined by Talairach space. Therefore, landmarks used in previous studies were used to identify the area of the medial wall activated in the ‘phantom on’ – ‘phantom off’ contrast.

Discussion
A number of theories have attempted to explain the phenomenon of the post-amputation phantom limb since the first published account by Mitchell in 1871 (Melzack, 1990; Ramachandran, 1993; Spitzter et al., 1995). In the main, previous studies have proposed that reorganization of the primary somatosensory cortex is primarily responsible for phantom sensations. In contrast, there have been fewer attempts to suggest mechanisms underlying supernumerary phantom limbs, perhaps due in part to their scarcity (e.g. Halligan et al., 1993, 1995). The findings of our fMRI study suggest that activity within areas traditionally classified as parts of the motor system can, under pathological conditions, influence the conscious perception of the body. The specificity of E.P.’s illusion suggests that either action- or sensory-related signals that were previously responsible for her perception of the arm in its last position are responsible for her ghost arm. While constant tactile stimulation of the left arm can prevent the appearance of the ghost arm, it is unlikely that E.P.’s illusion is driven primarily by proprioceptive influences, as her experience of the ghost arm is only updated after a new volitional movement. Thus, the experience of the ghost arm may rely more on action than perception.
The SMA and goal-directed movements

The SMA is a functionally complex area that is involved in many aspects of motor control (Tanjи and Shima, 1996). As well as reciprocal connections to M1, in the monkey the SMA proper (F3; Luppino et al., 1993) receives afferent projections from the cingulate motor areas, the pre-SMA (F6) and the parietal area PEci (initially defined by Pandya et al., 1982). As befits an area with such a diverse pattern of corticocortical connections, there have been a number of specific hypotheses concerning the function of the SMA. Most of these hypotheses have focused on the role of the SMA as a ‘supramotor’ area (Passingham, 1995; Tanji and Shima, 1996). Prominent amongst these have been the ideas that the SMA proper is preferentially involved in (i) the internal generation of movement in the absence of external cues (Chen et al., 1995) and (ii) the generation of planned sequences of movements (Tanjи and Shima, 1996). While it is possible that the activation of SMA seen in the present study may be indicative of either of these underlying roles, the specificity of E.P.’s percept argues for a distinct expression of one of the SMA’s functions.

According to some computational models of motor control, internal representations of future motor actions can be used as feed-forward controllers during movement execution (Wolpert and Ghahramani, 2000). For example, one model of saccadic eye movement (Robinson, 1975) has suggested that the route to a particular position is computed in a dynamic fashion by comparing the current position of the eyes with their intended target position (or ‘goal state’). The encoding of the end-point of a sequence is consistent with the proposed role of the SMA in the construction of internal representations of subsequent movements.

As well as evidence for the role of the SMA in the representation of future movements, there is also evidence that the origin of a movement may be represented by medial wall structures. Using single-cell recording techniques in monkeys, Clower and Alexander (1998) examined pre-SMA and SMA neurones during a sequential movement task. They found that SMA neurones selectively encoded specific spatial features of the simple joystick movements used (the origin, direction and end-points of movement). These effects were equally prevalent across each of the components of the movement task—the delay period (when the movement goal was specified), the reaction time period (between the delay and movement onset) and the movement period (the time from movement onset to target capture), although fewer SMA neurones still encoded the origin of the movement during the movement period.

Physiological interpretation of sustained SMA activity

If the origin of a movement remains represented after movement execution, this information may be the physiological substrate of E.P.’s perception of her phantom. While the long delay before E.P.’s phantom is experienced is hard to explain, there have been previous reports (Wolpert et al., 1998) of patients with deficits in the perceived position of their arm that are expressed after similar delays. While the patient of Wolpert and colleagues suffered from a perceptual deficit that can be viewed as a gradual corruption of a previously accurate estimate of the position of her arm, E.P.’s percept seems to be driven by the influence of a previously implicit computation of the motor system that reappears over time.

While this explanation is consistent with the behavioural expression of E.P.’s ghost arm, it is more difficult to describe in neurophysiological terms how a sustained representation may influence perception. However, there is no reason to believe that the mechanisms underlying E.P.’s percept are any different from those underlying other ‘positive’ perceptual illusions. For example, fMRI studies of the visual motion after-effect have found activation of area V5/MT (Zeki et al., 1993; Tootell et al., 1995). This is a significant observation as this area is thought to process afferent-driven visual motion (Zeki, 1974). The SMA is not traditionally regarded as a sensory area, but this does not mean that it cannot influence conscious perception of limb position. Using PET, Naito and colleagues (Naito et al., 1999) found activation of the SMA, CMA, premotor cortex and M1 during subjects’ perception of a kinaesthetic illusion. Activation of classical motor areas can therefore influence the perception of the limbs in space.

It is arguable that other aspects of the present paradigm may be responsible for sustained activity in the SMA. Previous functional imaging studies have described sustained activity in the medial wall during working memory tasks (e.g. Paulesu et al., 1993; Courtney et al., 1996; Fiez et al., 1996; D’Esposito et al., 1998). While the interpretation of this activity varies, it is generally taken to represent a form of motor preparation. The Talairach coordinates of the maxima from these studies place the peak activations within the pre-SMA, as the maxima are anterior to the VAC line (Petit et al., 1998).

It is unlikely that the sustained activity of the SMA proper seen in this study can be attributed to motor preparation, for two reasons. First, the anatomical location of the medial wall cluster is too posterior to be located within the pre-SMA. Secondly, it is unlikely that E.P. experienced any differences in motor preparation or in the selection of motor responses from memory between the two delay periods. E.P.’s left arm movements in both were stereotypical and followed a similar pattern—a brief movement after a vocal cue. This cue was identical in the two delay periods.

A further possible interpretation of the difference in sustained SMA activation is the difference of context between the button-presses that precede both tonic periods. In the movement before the ‘phantom on’ period, E.P.’s movement was self-initiated. In the other event, E.P. was instructed to move her right index finger in response to an external cue—a verbal instruction. It could therefore be argued that the differences in sustained SMA activation that
we observed reflect the internal or external nature of the instructions given to E.P. (e.g. Deiber et al., 1999). However, the multiple regression model used for analysis meant that differences between ‘phantom on’ and ‘phantom off’ tonic periods were analysed after the variance that could be explained by the modelled responses to the right-hand index finger movements had been removed. Finally, the sustained activation observed in the SMA may have been caused by E.P. attending to the phantom arm after it had appeared, as opposed to the SMA activity causing the phantom perception itself. It is difficult to dismiss this claim without examining explicitly the effect of attention to the phantom on the SMA activity. Our interpretation of the sustained activity is that it reflects condition-explicit changes in the BOLD signal of the right SMA that are specific to E.P.’s percept.

There is a great deal of evidence to suggest that normal subjects are usually unaware of many aspects of their actions, including the eventual goal of a movement (Fourneret and Jeannerod, 1998), yet this may not always be so. Focusing on the desired goal of an action, Jeannerod (1994) suggested that neurones encoding the ‘final configuration’ of the body would continue firing ‘until the final goal has been reached’. If the goal were not reached, ‘the sustained discharge would be interpreted centrally as a pure representational activity and give rise to mental imagery’ (Jeannerod, 1994). We believe that, in E.P.’s case, the sustained activity in the SMA may represent a neurovascular correlate of Jeannerod’s hypothesis. Our interpretation is that the sustained activity in SMA represents the origin of the movement. Thus, E.P. experiences two positions of the arm simultaneously, one representing where the arm was previously (its origin) and one representing its current position (its goal). Upon making a new volitional movement, the current position of E.P.’s arm becomes the origin of the movement, and thus (after a delay) upon completion of the new movement the ghost arm appears in the previously vacated position.

It is more difficult to ascertain the relationship between E.P.’s symptoms and the location of her lesion, which includes the left pre-SMA and cingulate motor areas. Previous experimental studies have implicated the pre-SMA as involved in motor inhibition: direct subdural stimulation of this area has been shown to terminate ongoing motor movements (Lüders et al., 1995). It is conceivable that a pre-SMA lesion could disinhibit an internal representation of a motor command in the manner suggested above. However, there is no obvious explanation from our data why the origin of the movement is retained and re-expressed after this delay, or why proprioception is not sufficient to cancel it, yet vision of the limb is. A further possibility is that E.P.’s ghost may arise from a loss of the normal influence of the cingulate motor areas on the SMA, as her lesion also includes these regions. Just as utilization behaviour [a behaviour observed after frontal lesions in which visual presentation of objects compels patients to grasp/use them (Lhermitte et al., 1983)] reflects the inability to suppress effects of the external world (the ‘affordances’ of objects) on the motor system, E.P.’s phantom percept may be an example of her inability to suppress the influence of internal representations on perception.

In a previous study (Hari et al., 1998), E.P.’s median nerve somatosensory evoked magnetic fields (SEFs) were found to be significantly weaker in the left secondary somatosensory cortex (SII) when the ghost arm was present. The authors concluded that this activity was an objective correlate of the ghost, consistent with SII’s postulated role in sensorimotor integration (Huttunen et al., 1996). We did not find SII activity in the current study when examining the results of the ‘phantom on’ – ‘phantom off’ contrast. However, failure to identify activation cannot be interpreted as proof that a given area plays no part in a given experimental challenge. There may be a number of reasons for the difference in results between the two studies. For example, the fMRI study was designed to maximize the low-frequency, tonic neurovascular activity associated with the ghost percept. The previous MEG study was designed to be maximally sensitive to stimulus-locked, higher-frequency differences in tactile-evoked SEFs. Thus, the experimental paradigms used in the two experiments were necessarily different. To permit formal comparison, it would be necessary to examine the differences in the event-related fMRI response to tactile stimulation in a similar manner to that performed in the MEG study.

Conclusions
The data presented in this paper demonstrate that sustained activity in a traditionally motor area of the brain (the SMA) correlates with E.P.’s perception of a third, phantom arm that she perceives in addition to her real left arm. Many investigations of body schema illusions do not progress beyond a discussion of the maps within the primary somatosensory cortex that represent a perceptual space—the body surface. The present results suggest that, while a perceptual space such as the somatosensory map can be used to influence the subjective position of the limbs, an ‘action space’, specified in terms of the contents of the motor system, can be used to generate a similar mapping. While our results say less about the mechanisms by which the body schema is constructed under normal conditions, they demonstrate that a seemingly unitary percept in both time and space can be generated from a combination of quite disparate sources of information about the past, present and future states of an organism.

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