Persistent hand motor commands in the amputees’ brain

Karen T. Reilly,1,2,4 Catherine Mercier,1,2 Marc H. Schieber3,4 and Angela Sirigu1,2

1Institut des Sciences Cognitives, 2Université Claude Bernard Lyon 1, Lyon, France, 3Department of Neurology and 4Department of Neurobiology and Anatomy, University of Rochester, Rochester, NY, USA

Correspondence to: Dr Angela Sirigu, Institut des Sciences Cognitives, CNRS, 67, Boulevard Pinel, 69675 Bron, France
E-mail: sirigu@isc.cnrs.fr

The loss of a limb leads to sensorimotor modifications that are frequently accompanied by the vivid experience that the missing limb is still present, and that it can be moved at will. Furthermore, amputees can clearly distinguish between phantom movements of the fingers and of more proximal joints, like movements of the elbow. This phenomenon raises the question of whether these specific phantom movement experiences are translated into differentiated activity within the remaining muscles. We recorded stump muscle activity when above-elbow amputees voluntarily moved their phantom limb. Voluntary movements of the phantom hand triggered specific patterns of stump muscle activity, which differed from activity recorded in the same muscle groups during movements of the proximal limb. This result indicates that the brain’s motor areas can be differentially activated according to the phantom movement the patient intends to perform, and suggests that hand motor commands are preserved after amputation. To further understand the interaction between central commands and sensory feedback in the perception of phantom movement we also measured stump muscle EMG activity in an amputee experiencing a frozen phantom limb, and in three below-elbow amputees with vivid phantom movements after inducing an ischaemic block. Failed attempts to move the paralysed phantom limb always resulted in the same EMG pattern, no matter what type of phantom movement was attempted, while ischaemic nerve block reduced or eliminated the ability to voluntarily move the phantom limb and produced a dramatic reduction in the amplitude of stump muscle EMG activity. Our data suggest that the experience of phantom hand movement involves the activation of hand motor commands. We propose that preserved hand movement representations re-target the stump muscles to express themselves and that when these representations are voluntarily accessible they can instruct the remaining muscles to move in such a way as if the limb is still there.

Keywords: amputation; phantom limb; motor command; hand; motor cortex

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Introduction

It is now well known that loss of a limb leads to modifications in the sensorimotor system and that these changes are frequently accompanied by the vivid experience that the missing limb is still present, and that it can be the object of mechanical, thermal and, unfortunately, painful sensations. A lesser known phenomenon, but one which is experienced by many amputees, is that the phantom limb can often be moved at will (Kooijman et al., 2000). What does it mean to move a limb that is no longer present? Phantom movement might represent a form of motor imagery with activity exclusively in the CNS, but preliminary evidence suggests that this is not the case, and that phantom movement actually involves some form of motor execution. For example, when Dhillon et al. (2004, 2005) asked amputees to voluntarily move their phantom hand they recorded activity in severed motor nerve fibres within the stump. This suggests that when amputees voluntarily move their phantom they generate activity in the nerves that previously supplied the missing limb. This activity is not only restricted to severed nerves, however, as Ramachandran (1993) observed stump muscle contractions in an above-elbow amputee during voluntary phantom finger movements. Together, these observations show that neural activity associated with the sensation of voluntarily moving the phantom limb is not restricted to the CNS, but also includes activity in peripheral motor pathways.

In a transcranial magnetic stimulation study of upper-limb amputees (Mercier et al., 2006), we showed...
that artificial stimulation of the motor cortex can elicit phantom limb movements. This result suggests that, despite the apparent ‘invasion’ of the remaining body parts into the cortical area that previously controlled the now-missing limb, movement representations of the missing limb are retained within the motor cortex. We wanted to know whether the sensation of making a range of distinct phantom limb movements arises from the activation of these preserved movement representations. To investigate this, we recorded stump muscle activity when upper-limb amputees voluntarily produced a range of distinct phantom limb movements. We hypothesized that different phantom movement intentions will activate different phantom movement representations that will give rise to the sensation of distinct phantom movements and the presence of distinct activity patterns in stump muscles.

**Material and methods**

**Subjects**

This study consisted of three separate experiments. In total, eight upper-limb amputees who had traumatic amputations 2.5–31 years earlier participated in this study: four above-elbow, three below-elbow and one at the level of the shoulder. Amputees reported that the presence of their phantom limb was associated with phantom pain ranging from none at all to severe. Patient characteristics are detailed in Table 1. The study protocol was approved by the Research Subjects Review Boards of the University of Rochester Medical Center, Rochester, NY, and the Local Ethical Committee, Centre Léon Bérard, Lyon, France. All subjects provided written informed consent to participate in the study.

**Table 1 Patient characteristics and phantom limb features**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Time since amputation (years)</th>
<th>Amputation level (above/below elbow)</th>
<th>Stump length (cm)</th>
<th>Daily prosthesis use</th>
<th>Number of distinct voluntary phantom movements*</th>
<th>Phantom limb pain†</th>
<th>Residual limb pain</th>
</tr>
</thead>
<tbody>
<tr>
<td>GP</td>
<td>2.5</td>
<td>Above</td>
<td>7</td>
<td>Never</td>
<td>4</td>
<td>5/10</td>
<td>None</td>
</tr>
<tr>
<td>RR</td>
<td>14</td>
<td>Above</td>
<td>24</td>
<td>Cable operated</td>
<td>12</td>
<td>none</td>
<td>None</td>
</tr>
<tr>
<td>JM</td>
<td>4.5</td>
<td>Above</td>
<td>15</td>
<td>Never</td>
<td>3</td>
<td>6/10</td>
<td>None</td>
</tr>
<tr>
<td>SF</td>
<td>2</td>
<td>Above</td>
<td>25</td>
<td>Myoelectric</td>
<td>2</td>
<td>6/10</td>
<td>None</td>
</tr>
<tr>
<td>SB</td>
<td>21</td>
<td>Below</td>
<td>27</td>
<td>Never</td>
<td>10</td>
<td>none</td>
<td>None</td>
</tr>
<tr>
<td>RS</td>
<td>9</td>
<td>Below</td>
<td>15</td>
<td>Myoelectric for first 8 months after amputation</td>
<td>11</td>
<td>6/10</td>
<td>4/10</td>
</tr>
<tr>
<td>JW</td>
<td>13</td>
<td>Below</td>
<td>8</td>
<td>Myoelectric for 1 year between 6 and 7 years after amputation</td>
<td>8</td>
<td>none</td>
<td>None</td>
</tr>
<tr>
<td>DB</td>
<td>12</td>
<td>Shoulder</td>
<td>No stump</td>
<td>Myoelectric for 1 year between 6 and 7 years after amputation</td>
<td>Cosmetic</td>
<td>8/10</td>
<td>None</td>
</tr>
</tbody>
</table>

*There was no significant correlation between stump length and the number of voluntary phantom movements each patient could produce (Spearman’s $r = 0.41, P > 0.05$).
†There was no significant correlation between stump length and the level of phantom limb pain (Spearman’s $r = -0.41, P > 0.05$).
and deltoid, as the contraction patterns in the pectoralis were near-identical to those in the deltoid. For subject SF (Fig. 4) we positioned electrodes over biceps, triceps and brachialis.

For every movement subjects were asked to move the phantom and intact limbs simultaneously. The instructed movements were cyclic movements of elbow flexion and extension, hand opening and closing, wrist flexion and extension, thumb flexion and extension, or finger abduction and adduction. The range of motion of the phantom limb was frequently less than that of the intact hand, so subjects were instructed to move the intact hand through the 'same range of motion and at the same speed that the phantom hand is capable of moving'. The approximate ranges of motion were between 5° and 20° for phantom elbow flexion [4–14% of normal range of motion (ROM)]; between 30° and 70° for wrist flexion/extension (20–50% normal ROM); and between one-fourth closed to fully closed for hand opening/closing. All movements were self-paced and subjects were asked to verbally report changes in movement direction throughout the trial, for example, changing from wrist flexion to wrist extension, which were entered into the data stream as keyboard markers and recorded together with the glove and EMG data. Each type of movement was tested in a separate trial and the order of the trials was randomly varied. A single trial lasted between 30 and 60 s, corresponding to ~10 movement cycles. The speed at which each subject could move their phantom limb varied. Phantom pain clearly affected the speed of voluntary phantom limb movements. For the above-elbow amputees, those who reported higher levels of phantom pain (JM, GP, SF) had an average movement speed of 3, 5 and 6 cycles/min, whereas RR reported low levels of phantom pain and had an average movement speed an order of magnitude faster (30 cycles/min). Similarly, the three below-elbow amputees all reported little to no phantom limb pain and had average movement speeds of ~25 cycles/min.

Electrodes, 10 mm in diameter (VerMed, Bellows Falls, VT, USA), were placed in a bipolar configuration over each muscle, such that the signal from the target muscle was optimized. EMG activity was amplified by a factor of 5000–20 000 to produce a signal that fell within a ±5 V range. A right- or left-handed instrumented glove (Cyber-Glove, Virtual Technologies, Palo Alto, CA, USA) was placed on the intact hand and it measured changes in joint position of the fingers and wrist. Spike2 software and a Micro 1401 interface (Cambridge Electronic Design, Cambridge, UK) were used to collect glove data and surface EMG simultaneously. Each glove sensor was sampled at the maximum rate of 78 Hz and EMG was sampled at 1000 Hz.

Off-line, EMG data were high-pass-filtered at 10 Hz to remove movement artefact, low-pass-filtered at 30 Hz to produce a smooth signal and rectified. Movement direction transition times were inserted into the data stream (see below for details) and all data shown are EMG traces of three movement cycles. Off-line, glove data were low-pass-filtered at 6 Hz. For each trial we used data from only one sensor: the one that best characterized the movement on that trial, for example, the wrist flexion/extension sensor for wrist movements or the thumb metacarpophalangeal (MCP) joint sensor for thumb movements. Sensor data were not transformed into joint angles, as the absolute joint excursion was less important than the cyclic nature of the movement, but previous studies have shown that glove sensor output is linearly related to joint position (Lang and Schieber, 2003).

The sensor that best captured the cyclic movement was chosen by visual inspection of all 22 glove sensors and the angular velocity at each point in time throughout the trial was calculated for this sensor. The times of zero velocity were identified as times at which the movement cycle switched directions (i.e. between flexion and extension). If none of the sensors captured the movement (either because the movement was too small or because it was not detected by the glove i.e. elbow flexion and extension) transitions in the EMG as well as verbal event markers included in the data stream at the time of testing were used as a guide for the manual insertion of markers indicating movement transition times. All movement direction transition times are shown as dashed horizontal lines in the figures.

The repeatability of EMG patterns associated with phantom limb movements was assessed by asking the amputees to execute the same movement at two different times in the same testing session (GP), or on separate days (RR, JM).

Results and discussion

Figures 1–4 show the EMG activity from the amputated and intact sides of four above-elbow amputees as they made three distinct movements simultaneously with both their intact and phantom hands. The first column of each figure shows EMG activity associated with elbow flexion and extension. On the amputated side of all four patients the biceps and triceps produced a reciprocal pattern of activity appropriate for flexion and extension of the (non-existent) elbow, while the deltoid (GP, RR) and the brachialis (SF) showed bursts of activity during both the flexion and extension phases of the phantom movement (double bursting). On the intact side, the activity in the biceps and triceps was also appropriate for elbow movement, but was not as clearly modulated as on the amputated side. The absence of clear modulation of the activity on the intact side can be explained first by the fact that the intact elbow moved freely in space while it required a large effort to move the phantom elbow, as all amputees reported that they felt they were moving their phantom against resistance. Thus, the intact arm EMG activity was associated with an isotonic movement while the phantom arm EMG activity more closely resembled isometric contractions, which in normal subjects are associated with higher EMG levels and clearer between-phase modulations than isotonic contractions. The second explanation for the absence of clear EMG modulation on the intact side during elbow movements is that the range of motion of the phantom elbow was very small, varying...
between ~5 and 20°. Thus, there was very little movement of the intact elbow, because subjects were instructed to match the movements of their intact limb with the capacity of their phantom limb.

For all four amputees phantom hand movements were accompanied by EMG activity in muscles that would never have contributed to hand movements before the amputation (biceps, triceps, deltoid and brachialis). The second and third columns of Figs 1–4 show, for example, that during phantom hand opening/closing, thumb flexion/extension, wrist flexion/extension and finger abduction/adduction proximal arm muscles on the amputated side were active, despite the fact that none of these muscles normally move the joints of the hand, as shown by the absence of movement-related activity in these muscles on the intact side. Interestingly, in all four subjects this activity was not characterized by a fixed relationship between stump muscles; instead muscle co-activation patterns changed as a function

**Fig. 1** Raw EMG and kinematic profiles for patient GP executing three distinct cyclic bilateral movements. Instructed movement is noted above each column and movement phase is indicated as F (flexion), E (extension), O (opening) or C (closing). EMG has been scaled to maximize clarity, with EMG from a single muscle on the same scale but different scales for all six muscles.

**Fig. 2** Raw EMG and kinematic profiles for patient RR executing three distinct cyclic bilateral movements. Instructed movement is noted above each column and movement phase is indicated as F (flexion) or E (extension). EMG has been scaled to maximize clarity, with EMG from a single muscle on the same scale but different scales for all six muscles.
of the movement. For example, in patient RR (Fig. 2), biceps and triceps were activated reciprocally during flexion-extension of the phantom elbow, whereas they co-contracted during opening–closing of the phantom hand. Looking across the three movements performed by each subject, it is clear that not only were there unexpected activations in proximal arm muscles during phantom hand movements but the patterns of activity in the amputated muscles differed according to the phantom movement executed. For example, in patient JM (Fig. 3), during opening and closing of the phantom hand both the triceps and deltoid muscles were phasically modulated, with more activity during hand closing.
than opening, while the biceps showed spontaneous discharges that were unrelated to the phantom movement. In contrast, during flexion and extension of the thumb the biceps and triceps were both phasically modulated in a reciprocal manner, with biceps producing much more activity during thumb extension than flexion, and the triceps producing slightly more during thumb flexion than extension. In all four patients distinct movements of the phantom limb were associated with distinct patterns of EMG activity in the remaining stump muscles, whereas the same movements produced little or no EMG modulation on the intact side.

We observed a similar association between distinct phantom limb movements and distinct EMG patterns in three below-elbow amputees (Fig. 5). These subjects differ from those in Fig. 1–4 in that they have retained most of the muscles that would have made these movements if the hand was still present. These data demonstrate, however, that despite the loss of the hand, and despite extensive post-amputation reorganization in the cortical motor representations of the stump muscles, amputees can still differentially activate their stump muscles during the production of distinct phantom limb movements.

Fig. 5  Raw EMG and kinematic profiles for three below-elbow amputees executing three distinct cyclic bilateral movements. Instructed movement is noted above each column and movement phase is indicated as F (flexion), E (extension), O (opening) or C (closing). Since these subjects are below-elbow amputees phantom hand movements are all associated with EMG activity in muscles that would have been active during those movements (unlike the activity observed in the stump muscles of above-elbow amputees). Thus, only EMG activity recorded from the amputated side during three movement cycles is shown, and this shows that distinct phantom movements were associated with distinct stump muscle EMG patterns. EMG has been scaled to maximize clarity, with EMG from a single muscle on the same scale but different scales between muscles. Note that because of different movement speeds the time scales for each subject differ.
If EMG patterns associated with particular phantom movements really represent the delivery of specific motor commands associated with a given movement intention, then we should expect these patterns to be reproducible over time. Figure 6 shows the EMG activity during one phantom movement from three above-elbow amputees recorded on different days (for patients JM and RR) and at the beginning and end of a 3 h testing session (for patient GP). This figure shows that the muscle contraction patterns associated with a given phantom limb movement.

**Fig. 6** Repeatability of EMG patterns recorded from the same patients shown in Figs 1–3. Each patient executed the same movement at two different times in the same testing session (GP), or on different days (RR, JM). For GP, EMG from the same muscle is on the same scale for both trials, but is different for each muscle. For RR and JM the scale is different for each muscle and each repetition.
were very stable across time. A similar finding was observed for other phantom limb movements although we do not show the data here. Thus, patients who report the ability to produce distinct phantom movements do not simply produce random contractions in their remaining muscles. Instead, when they have a specific phantom movement intention there is a distinct movement-related pattern of EMG activity, and this pattern can be reproduced over time, sometimes with months between testing sessions (JM and RR).

These results show that cortical motor regions are differentially activated during the production of different phantom movements. The selectivity and reproducibility of the EMG patterns indicate that there is an implicit a priori knowledge of which motor command will lead to which phantom movement, and that amputees do not simply send out a random command when asked to produce a particular movement. On the basis of these findings we suggest that the sensation that the phantom is moving arises from the voluntary activation of a distinct phantom movement representation in the motor cortex, which then results in a distinct EMG pattern in stump muscles. Following this view we would not expect to see distinct EMG patterns in the stump muscles of amputees with immobile phantom limbs. In the next experiment we test this hypothesis by examining the EMG activity patterns in stump muscles of one amputee with a ‘frozen’ phantom when he attempted to make a number of distinct phantom movements.

Experiment 2—EMG patterns during attempts to move a ‘paralysed’ phantom limb

Subjects and methods

DB had his right arm amputated at the level of the shoulder 12 years before the study. He reported the vivid presence of a complete phantom arm and hand that was completely ‘frozen’ in one position. We palpated the muscles of the trunk, proximal arm and face when he attempted to make a range of different movements of the phantom limb. These attempted movements were accompanied by muscular contractions in the pectoralis, latissimus dorsi, upper and lower trapezius, so we placed electrodes over these muscles in mirror correspondence on both sides of the body. (We do not show data from the lower trapezius muscles, as the contraction patterns were identical to those in the upper trapezius.)

We asked DB to attempt to move his phantom and intact limbs simultaneously. He reported that attempts to move his phantom limb resulted in the feeling that he was trying (unsuccessfully) to move against very strong resistance. Thus, he was unable to completely match the movement sensation of both limbs as the phantom limb never moved whereas the intact limb moved freely in space. As it was not possible to match the range of motion of the intact and phantom limbs (because the phantom limb was completely immobile), DB reported that he attempted to match the sense of effort required to move his two limbs.

Results and discussion

During each attempted phantom movement DB reported that no matter how much effort he used the phantom limb always remained in the same position. Figure 7 shows the EMG activity from the amputated and intact sides of the body when DB attempted to perform three distinct movements of his phantom limb. Similar to the above-elbow amputees who could voluntarily move their phantom limb (Experiment 1), when DB attempted to move his phantom elbow, wrist or hand there was always activity in proximal upper extremity muscles that would not normally be active during these movements. In contrast with the patients with mobile phantom limbs, however, the stump muscles of DB always contracted simultaneously; they never acted in a reciprocal manner, and the pattern remained the same regardless of which phantom movement was attempted. Interestingly, for the hand opening/closing and wrist flexion/extension movements DB also had movement-related activity in intact side proximal muscles. In normal subjects proximal arm muscle contractions are often observed during effortful contractions of distal hand muscles. Attempts to move the phantom limb were extremely effortful, inducing perspiration and a feeling of being very tired. Thus, since DB matched the sense of effort on the intact side with that of the amputated side, the intact side proximal muscle activity during distal movements reflects the enormous effort he expended to attempt to move his phantom limb.

These results show that the motor network controlling the hand is differentially activated during the production of different phantom movements, but not during failed attempts to move a paralysed phantom limb. Thus, the sense of being able to voluntarily move the phantom appears to be related to the amputee’s ability to activate distinct phantom movement representations in the motor cortex, which are then translated into the production of distinct patterns of EMG activity in the remaining muscles.

One issue that still remains, however, is whether the sensation of phantom movement arises solely from the efference copy of distinct motor commands, or whether it also relies upon sensory feedback generated by distinct muscle contraction patterns. This was tested in the next experiment where we induced an ischaemic block proximal to the stump of three below-elbow amputees and recorded EMG activity in the same muscles when they made voluntary contractions of their phantom limb before inflation, after inflation and after deflation of a blood pressure cuff positioned across the elbow of their amputated limb.
Experiment 3—EMG patterns during phantom movements and ischaemia of the stump muscles

Subjects and methods

Three below-elbow amputees [years since amputation: 31 (SB—left), 6 (RS—left) and 13 (JW—right)] participated in this experiment. All three subjects reported being able to move their phantom limb voluntarily, though the phantom movements were often effortful, slow and of small amplitude.

Owing to atrophy and post-amputation surgical procedures it was sometimes difficult to identify from exactly which muscles we recorded. In general, we recorded from two flexor and two extensor muscles of the forearm on the amputated side, and then placed electrodes in a mirror configuration over the muscles on the intact side. All electrodes were placed close to the elbow to make it easier to identify which muscles were generating the majority of the activity on the basis of their known anatomical origins. We recorded from the digit 5 portion of Flexor digitorum profundus (FDP), wrist extensors, wrist flexors, the flexor muscle mass (probably a combination of flexor digitorum superficialis and the two wrist flexors), the common finger extensor and, in one patient, from brachioradialis.

Subjects were seated with both elbows on a table; they made self-paced, cyclic, voluntary synchronous movements with their phantom and intact limbs such that their phantom and intact limbs moved with identical speed and amplitude. EMG activity was recorded from muscles on the intact and amputated sides of the body while movement kinematics of the intact hand were recorded using an instrumented glove.

After measuring the EMG activity associated with voluntarily phantom movements (pre-inflation trials) the blood pressure cuff was inflated to 200 mmHg and maintained within 200 ± 10 mmHg until cuff deflation. Before cuff inflation, and each 5 min after inflation, we asked subjects to close their eyes while cutaneous sensory thresholds near the tip of the stump were tested with von Frey filaments. We attempted to keep the cuff inflated until there was no sensation at the tip of the stump, but we were only able to achieve this in one patient, SB, who was unable to feel the largest von Frey probe after 15 min of cuff inflation (the cuff was deflated after 19 min). The other two patients reported that they were uncomfortable and asked for the cuff to be deflated after 14 (RS) and 30 (JW) min. At this time their sensory thresholds had decreased but they still had some sensation at the tip of the stump.

Results and discussion

All three amputees reported that the ischaemic block produced by inflation of a blood-pressure cuff across the elbow did not remove the sensation that the phantom limb was present. They also reported, however, that the longer the cuff was inflated the more difficult it became to move the phantom limb. Figure 8 shows the EMG activity in the stump muscles of all three patients as they made flexion extension movements of their phantom wrist before inflation, after inflation and after deflation. This figure shows that ischaemic block resulted in a total loss of EMG in the stump muscles (SB), or in a reduction in the amplitude of movement-related EMG but without any change in the pattern of this activity (RS and JW). These EMG changes were...
paralleled by the verbal reports of the patients of a complete loss of the sensation of phantom movement (SB) or a decrease in the amplitude of the movement (RS and JW). We examined the effect of the ischaemic block on a range of distinct phantom movements, and although we show data from only one movement the ischaemia-induced EMG changes were similar for all phantom movements.

After 10 min of cuff inflation SB said ‘I can still feel my phantom hand but it feels as though it is totally frozen in a block of ice’. RS reported that by the time the cuff was deflated all the movements had become very difficult and that he was completely unable to move his thumb, a movement that had been easy before cuff inflation. Finally, for JW, the cuff was inflated for 30 min, and across time he reported a gradual increase in the amount of effort required to make the phantom movements, and a decrease in the range of motion of the phantom hand until it eventually felt as though he could only move it through an extremely small range.

Our observation that ischaemic block following inflation of a blood pressure cuff around the elbow eliminates or reduces the ability to voluntarily move the phantom limb suggests that accessing the cortical representation and generating activity in descending motor pathways is not sufficient to give rise to the sensation of phantom limb movement. Instead, for the amputee to experience movement of the phantom limb the motor commands must arrive at the selected stump muscles in order to generate ascending afferent sensory feedback. It is important to note, however, that the amputee with the ‘frozen’ phantom limb also had access to sensory feedback, as attempts to move his phantom were always associated with contraction of stump muscles. Thus, access to sensory feedback from the stump muscles is not sufficient to experience the sensation that the phantom is

Fig. 8 Raw EMG and kinematic profiles for three below-elbow amputees executing three distinct cyclic bilateral movements before inflation, after inflation and after deflation of a blood pressure cuff positioned across the elbow. Only EMG activity recorded from the amputated side during three movement cycles is shown. EMG has been scaled to maximize clarity, with EMG from a single muscle on the same scale but different scales between muscles and subjects. Note that because of different movement speeds the time scales for each subject differ.
moving. Indeed, if this were the case then voluntary attempts to contract stump muscles could also give rise to phantom movement sensations, but none of the patients ever reported unexpected movement of the phantom when their intention was to contract stump muscles.

**General discussion**

We found that distinct movements of the phantom limb were associated with distinct patterns of EMG activity in the remaining stump muscles, and therefore that the cortical motor network controlling the hand was differentially activated during the production of different phantom movements. The selectivity and reproducibility of the phantom-movement-related EMG patterns indicate that there is an implicit a priori knowledge of which motor command will lead to which phantom movement, and that amputees do not simply send out a random command when asked to produce a particular movement. Our control studies with an amputee with a ‘frozen’ phantom limb and ischaemic block of the stump muscles suggest that the ability to voluntarily move the phantom limb requires the activation of preserved motor cortical movement representations resulting in activity in both descending motor and ascending sensory pathways. From this perspective the neural basis underlying the sensation of movement of the phantom limb appears to be no different from that underlying voluntary movement of an intact limb, as studies in curarized limbs show that the efference copy generated by delivery of a motor command is not sufficient to give rise to a sense of movement (McCloskey et al., 1978). The idea that common neural circuits underlie the processing of both phantom and intact limb movements is also supported by the results of functional imaging studies in amputees making voluntary movements of their phantom and intact limbs (Ersland et al., 1996; Willoch et al., 2000; Hugdahl et al., 2001; Rosen et al., 2001).

Many studies have shown that after limb amputation movements of the remaining stump can be evoked from primary motor cortical sites that were formerly devoted to movements of the now-missing limb (Donoghue and Sanes, 1988; Hall et al., 1990; Sanes et al., 1990; Cohen et al., 1991; Ojemann and Silbergeld, 1995; Pascual-Leone et al., 1996; Schieber and Deuel, 1997; Wu and Kaas, 1999; Qi et al., 2000). The traditional view of this amputation-induced expansion of stump motor cortex muscle territories has been that it occurs at the expense of the missing limb’s motor representation. We suggest instead that this reorganization permits the disconnected cortical representation of the missing limb to maintain interactions with the periphery, gaining access to efferent targets and to afferent feedback, and that this re-routing contributes to the survival of cortical representations of phantom limb movements. Such re-targeting of missing-limb-related efferent activity towards the remaining stump muscles is consistent with the observation that cortical neurons that previously targeted motoneurons in the missing muscles can re-target motoneurons in the remaining stump muscles, and that deprived motoneurons previously supplying hand muscles can find new muscle targets in stump muscles (Wu and Kaas, 2000).

Our clinical interviews revealed that those amputees who could move their phantom limb voluntarily had the ability to make a large range of voluntary movements soon after the amputation, but that over time the range of motion of the phantom and the number of movements that they could produce decreased, in some cases resulting in a completely frozen phantom. It is unclear which factors interfere with the preservation of a closed sensorimotor loop, in which the intention to move the phantom limb results in contraction of a muscle target that in turn gives rise to afferent feedback. The amputee we studied who said his phantom limb was paralysed had a higher-level amputation than the other amputees. It is possible that because of the very proximal level of his amputation there was insufficient survival of motoneurons and primary afferents, and thus post-amputation reorganization did not result in the maintenance of appropriate sensorimotor loops for control of the now-missing limb. The fact that attempted movements of the paralysed limb resulted in stump muscle contractions suggests that there was some functional re-mapping between the cortical representation of the missing limb and the stump muscles. Even though survival of a minimum number of motoneurons and primary afferents is probably necessary to voluntarily move the phantom limb, this alone does not appear to be sufficient. Instead, the fact that attempts to make different movements of a paralysed phantom limb do not result in different EMG patterns in stump muscles suggests that the ability to voluntarily move the phantom requires that re-mapped connections to and from the sensorimotor periphery be controlled selectively by cortical motor representations that can be voluntarily accessed.

Frequent use of a myoelectric prosthesis and low phantom pain levels are positively correlated with reduced cortical reorganization (Flor et al., 1995; Lotze et al., 1999, 2001; Karl et al., 2001, 2004). Since we did not directly investigate cortical reorganization in our patients it is difficult to know whether the ability to voluntarily move the phantom limb is also correlated with the degree of cortical reorganization. What we can say, however, is that distinct EMG patterns in stump muscles during distinct phantom limb movements were observed both in patients with and without frequent use of a myoelectric prosthesis, and in patients with and without phantom pain.

A better understanding of the factors affecting voluntary access to amputated limb movement representations might have implications at the clinical level for the control of phantom pain and for the use of prosthetic limbs. Assisting amputees in ‘re-awakening’ their phantom limb movement representations might be a potentially useful tool in the management of phantom limb pain, as studies have demonstrated that increasing the ability to move the phantom limb can reduce pain (Ramachandran and Rogers-Ramachandran, 2006).


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Phantom movement motor commands


