Interdependence of movement and anatomy persists when amputees learn a physiologically impossible movement of their phantom limb

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The feeling we have of our own body, sometimes called ''body image,'' is fundamental to self-awareness. However, by altering sensory input, the body image can be modified into impossible configurations. Can impossible movements of the body image be conjured solely via internally generated mechanisms, and, if so, do the structural characteristics of the body image modify to accommodate the new movements? We encouraged seven amputees with a vivid phantom arm to learn to perform a phantom wrist movement that defied normal anatomical constraints. Four reported success. Learning the impossible movement coincided in time with a profound change in the body image of the arm, including a sense of ownership and agency over a modified wrist joint. Remarkably, some previous movements and functional tasks involving the phantom arm became more difficult once the shift in body image had occurred. Crucially, these introspective reports were corroborated by robust empirical data from motor imagery tasks, about which amputees were naïve and to which assessors were blind. These results provide evidence that: a completely novel body image can be constructed solely by internally generated mechanisms; that the interdependence between movement repertoire and structural constraints of the body persists even when the structural constraints imparted by the body do not—the body image we construct still constrains imagined movements; and that motor learning does not necessarily need sensory feedback from the body or external feedback about task performance.

body schema | sensorimotor learning

The feeling that we have of our own body, its size and shape and that we own it, constitutes a fundamental aspect of self-awareness (1). This bodily awareness, first coined "body schema" (2) and labeled here as "body image," is thought to be in part innate and in part constructed, and modified, by ongoing proprioceptive input from the body (3). Although it is often taken for granted, body image is disrupted in a range of neurological and psychiatric conditions (see ref. 4 for a list of conditions) and can be readily disrupted experimentally in healthy volunteers by changing proprioceptive input (5, 6), inducing a visual–tactile conflict (7, 8), or, in nonamputees with arm pain, by distorting the visual appearance of a limb (9). In each experimental case, body image is disrupted by modifying sensory input. The potent influence of sensory feedback on body image is demonstrated by the induction of impossible configurations of the body image. For example, a blindfolded participant places the palm of their own hand on their forehead. The tendon of the muscle that straightens the elbow is vibrated at ≈70 Hz, which induces the illusion in the participant that they can feel their elbow bending, which in turn feels as although their hand is moving backwards through their own head (5).

Such remarkable manipulations of body image highlight two fundamental questions that remain unanswered: (*i*) Can body image be modified solely via internally generated mechanisms? and (*ii*) Are the principles that govern the relationship between body image and movement repertoire in the human brain simply a reflection of the Newtonian limitations of the human body or do they persist when the movement and body image is purely representative? Investigation of such issues has been problematic because it is impossible to avoid reporting bias from participants, and pure introspective report does not necessarily elucidate the mechanisms underlying an experience. Here, we overcame this problem by using two motor imagery tasks, both known for their powerful property to qualify and quantify implicit motor behavior/execution. Importantly, participants remained naïve to the true purpose of these measures. Seven arm amputees with a vivid sense of their phantom arm, or an "intact body image" of their phantom arm (see Table 1) learned a particular arm movement that defied normal biomechanical constraints of the arm—thus it was an "impossible" movement. The first motor imagery task that measured implicit motor execution was a left/right hand judgment task, in which one is shown images of a human hand and is required to make speeded judgments as to whether the hand is a left hand or a right hand. There is a large amount of data from this test that demonstrate that response time relates very closely to the extent of rotation required to move one's own hand from where it rests to a posture that matches the one shown in the image. That is, correct left/right hand judgments require the participant to mentally rotate their own hand to match that shown in the picture (10). We included pictures that showed a hand in the posture at either end of the impossible movement. We included trials in which participants held their phantom hand in one of those postures. By so doing, we were able to show decreased response times that were movement-specific, limb-specific, and image specific. Importantly, such a decrease was observed only in those participants who reported success at learning the impossible movement. Those people also reported profound shifts in the structural characteristics of their phantom arm. The second motor imagery task involved participants reporting the apparent motion path between two alternating images, showing a hand at either end of the impossible movement. The normal response is to perceive the hand moving between the two positions through the impossible movement until the interval between images is ≈1 sec long, at which stage one perceives the long physiological movement. Using this task, we corroborated the abovementioned results by showing that before training, all participants reported a normal response for images of either hand, but after training, only the four successful participants, and only for

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Table 1. Participant characteristics

Ss	Aff/dom	Sex/age	MOI	Site	Phantom	Years since amp.	Days to success or quit	Vivid phantom	Vivid mov't
1	l/r	m/35	trau	BEA	Intact	1	21	4	0
2	l/r	f/42	surg	AEA	Intact	7	14	7	0
3	r/r	m/64	trau	AEA	Short forearm	24	20	3	0
4*	l/r	m/23	surg	AEA	Short forearm	1	14	4	6
5*	r/r	m/21	trau	AEA	Intact	1	6	9	9
6*	r/l	f/34	trau	AEA	Short forearm	6	13	8	8
7*	l/r	m/33	surg	AEA	Intact	12	28	7	5

Ss, subjects; Aff, arm amputated; dom, dominant limb before amputation; MOI, mechanism of injury; Site, location of amputation; BEA, below elbow; AEA, above elbow; amp., amputation; Vivid phantom, distance from left anchor of participant's mark on a 10-cm visual analogue scale, in answer to the question: "How vivid is the feeling of a phantom limb?"; Vivid mov't, distance from left anchor of participant's mark on a 10-cm visual analogue scale, in answer to the question: "How vivid is the movement when you move it the short way?"

*Marks those participants who reported success in learning the impossible movement.

pictures of their amputated side, perceived the short impossible movement regardless of the interval between images.

Results

Participant Reports. After training, four participants reported success (Table 1). When asked how they attempted to learn the movement, all participants reported that they used visual imagery and that they tried to see the hand spinning the wrong way on their forearm. Initially for successful participants, and throughout training for unsuccessful participants, they reported that it felt like they were observing someone else's arm, or that their visualized phantom didn't feel like theirs. Remarkably, all four successful participants reported that after repeated practice, they felt a change in their phantom arm and that this change coincided in time with the feeling that they were indeed performing the new movement and were doing so with their own phantom arm, rather than an external model or a phantom limb that belonged in part to someone else.

For all four successful participants, this change in their phantom limb constituted the development of a new phantom wrist joint that permitted the impossible movement. One described a planar joint. He also reported stiffness in this new joint and muscle fatigue in his phantom forearm if he practiced the task for too long. He also reported that, whereas he could previously move his phantom hand side to side (he demonstrated this movement by radial and ulnar deviation of his opposite hand), that movement was now difficult to do because of the new shape of his phantom wrist. Another participant described a joint that felt as if it had a shape similar to his shoulder joint (that is, consisting of a convex and a concave surface). Two participants described a novel articulation that involved an axis protruding into the hand, on which the hand could freely rotate. Both of these participants also reported that sideways movement of the phantom hand at the wrist had become more difficult. One of these participants renovated an old prosthesis to make its hand twist freely on its forearm. Watching this movement allowed him to "work out how to do the movement himself." He drew what his new wrist felt like (Fig. 1*C*).

Reaction Time on Left/Right Hand Judgments. Crucially, without exception, reaction time data corroborated participant report. Before training, mean reaction times reflected the structural constraints of intact arms: Reaction time was shorter when the position in which the hands were held matched the image than when it did not [main effect of posture, $F(2, 5) = 49.6, P < 0.001$]. All participants had shorter reaction times at final assessment than they had at initial assessment [main effect of time: $F(1, 6) = 11.2$, $P = 0.044$]. Reaction time was longer for pictures of the amputated limb than for pictures of the intact limb before training, but not after training [time × pictured limb: $F(1, 6) = 19.5$, $P = 0.021$]. That is, the longer reaction time for pictures of the amputated side, which is an established finding in amputees (11, 12), was no longer present after training. However, these participants were not faster overall [no main effect of success: $F(1, 6) = 1.2$, $P = 0.35$], but this change was driven by selective changes in reaction times for certain images in the four successful participants (time × pictured limb × success: $F(1, 6) = 20.3$, $P = 0.02$). That is, only the four successful participants became faster, but only for images of the amputated limb when their phantom hand position was opposite to that shown in the image, thus requiring a very long conventional movement, or the (very short) impossible movement, to mentally maneuver their phantom hand to match the image [four-way interaction: time × pictured limb × success × posture: $F(2, 5) = 12.4$, $P = 0.007$]. The side of amputation did not affect mean RT ($P = 0.24$). Reaction times also corroborated the report from the two successful participants that sideways wrist movement had become more difficult because of the altered shape of the phantom wrist (Fig. 1*D*). That is, response time for only these two participants was longer after training, only for images of the amputated side, which showed the hand deviated to one side.

Accuracy was >85% in all trials. There was no speed–accuracy tradeoff [logistic regression of response (correct or incorrect) vs. RT: χ^2 (1) = 0.15, $P = 0.70$].

Apparent Motion Path Task. To further corroborate participant report and our reaction time data from the left/right judgment task, we showed participants two alternating images, showing a hand at either end of the impossible movement (Fig. 1*B*). Before training, all seven participants reported the normal physiological movement of the hand when they were shown two alternating images of the hand at either end of the impossible movement, once the interval between images was >700 ms (Fig. 1*B*). This is consistent with data from healthy participants—one normally perceives the hand moving between the two positions through the long, physiological movement if the rate at which the two images alternate is equal to or slower than the speed at which they can perform the movement themselves (13). After training, the four successful participants perceived the impossible movement regardless of the rate at which images alternated but only for images of the amputated side. There was no change in response time for pictures of the intact side, and there was no change in response times for either hand for the three unsuccessful participants (Fig. 1*B*).

Participants spent an equivalent amount of time practicing the impossible movement and imagining the same movement on the

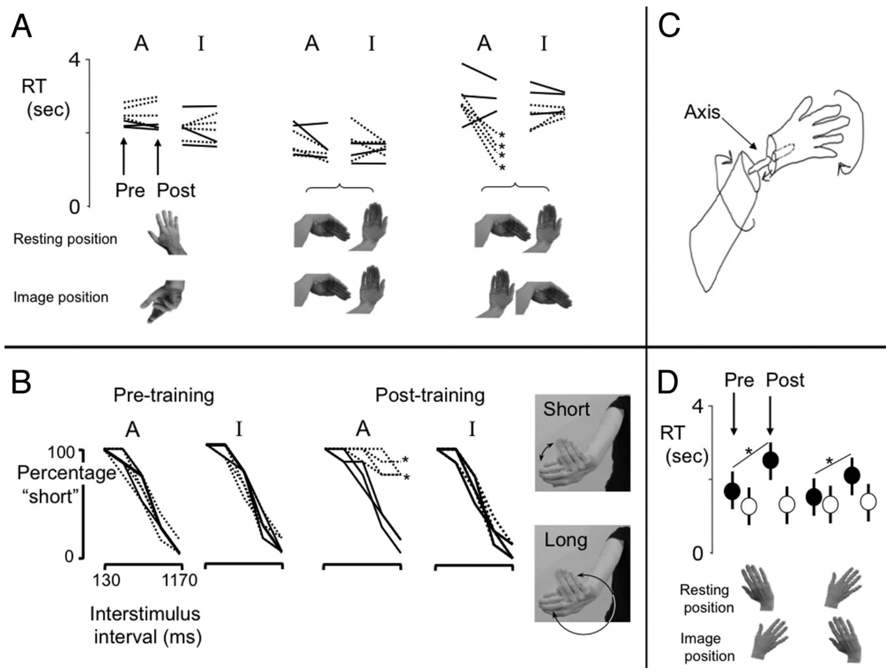

Fig. 1. Altered response times for motor imagery tasks corroborate participant reports. (*A*) Reaction time (RT, *y* axis) for correct responses on a left/right hand judgment task for different combinations of the resting position (upper line of images, ''resting position'') and the position of the hand shown in the image (bottom line of images, ''image position''), when pictures corresponded to the amputated side (A) or intact side (I). Participants responded by using a foot pedal, with left and right corresponding to depression of either the front or back of the foot. Individual mean RTs for before (Pre) and after (Post) training are shown. Dashed lines represent data from participants who successfully learned the impossible movement. Solid lines represent data from participants who did not. Asterisks mark significant decrease in RT between pre- and posttraining ($P < 0.01$). Note the decrease in RT after training when the resting and image position were at either end of the impossible movement, for successful participants' amputated side only. (*B*) Percentage of short-path choices in the apparent motion task in which participants were shown alternating images of a hand in the position at either end of the impossible movement. The photograph shows the short and long motion paths. The rate at which the images alternated ranged from 130 to 1170 ms, at 80-ms intervals, and was randomized and counterbalanced so that each rate was used eight times. At each flash rate, the images were shown until the participant responded. Asterisks mark those participants for whom the short motion path was seen regardless of the rate at which the images alternated—an indication that they had learned the impossible movement. Body image modifications during the learning of impossible movements: (*C*) The picture drawn by one successful participant, depicting the new axle he perceived in his phantom wrist joint. He drew permissible rotations of his phantom hand and forearm. Left/right hand judgment task data: (*D*) Mean and SD foot-pedal RT for the two participants (including the one whose drawing is shown in *C*) who reported the formation of a novel wrist joint involving the new axle. When the image showed a hand with the wrist bent in a manner that would be prevented by the axle, there was a longer RT at posttraining for the amputated arm (filled circles) but not for the intact arm (open circles). Asterisk denotes significance at $\alpha = 0.05$.

intact limb (not significant). There was no difference in practice frequency or duration between those who reported success and those who did not (*SI Text*).

Discussion

This study has two important findings. The first is that the feeling that we have of our own body, which constitutes a fundamental aspect of self-awareness (1), can be profoundly modified solely by internally generated mechanisms. There is a very large amount of literature that demonstrates the capacity of the human brain to change in response to sensory and external feedback (see ref. 14 for an early review)—our body image can be readily disrupted by modifying or removing proprioceptive feedback from, or about, a body part (15). That proprioceptive input can so readily disrupt our body image is considered important evidence that the body image in fact depends on such input (2). However, by inducing profound changes in body image related to the wrist via learning a formerly impossible movement of a phantom arm, we clearly demonstrate that modifications in body image do not necessarily depend on proprioceptive input. In fact, this finding extends our understanding of the brain's plasticity because it is evidence that profound changes in the mental representation of the body can be induced purely by internal brain mechanisms—the brain truly does change itself (16).

The second important finding relates to the accepted convention that sensorimotor actions are produced by transformations that use internal models of the mechanics of the body and the world (17). That learning of the impossible phantom movement coincided in time with the change in body image of the phantom limb, confirms the assertion that our movement repertoire and our anatomical structure are fundamentally linked (18) and extends it by demonstrating that this link governs, at a fundamental level, the representation of movement and the body in the human brain. Although the idea that the brain models Newton's laws has been proposed before (19), our results provide evidence that the interdependence of body's form and function persists when the brain constructs new movement and body representations without a physical substrate in the body.

Current opinion holds that sensorimotor learning occurs via the production of transformations that utilize internal models of the mechanics of the body and the world (17). There are compelling theoretical arguments that emphasize the importance of forward models, in which the brain predicts and simulates the outcome of a motor plan for sensorimotor learning (20). Internal comparison of predicted state and the outcome state permits correction of the error and subsequent adjustment of the motor plan. Critical to this conceptualization and crucial to the interpretation of the current results is feedback about the outcome of the motor plan (21). In the current study, participants had no sensory feedback from the limb. Although imagined movements are associated with fluctuations in muscle activity (22), preliminary testing detected no muscle activity distal to the shoulder, and all four successful participants had above-elbow amputations. Thus, no sensory feedback could have been interpreted as reflecting elbow or wrist movements. We propose that participants generated a visual image of the outcome state (that is, what the movement would look like had the motor plan been executed) and used comparison between this visual image and the predicted state to modify the motor plan. If so, this visual imagery seems to simultaneously modify the body image. That vision can modify the body image is established, and it has recently been shown that visually modified body image can impart top-down effects on the limb itself (9).

Insofar as the participants in this study learned a new task without executing that task with physical body components, the body of literature on mental practice (imagining that one is performing a movement or task when one is, in fact, not), seems relevant. However, a key distinction exists between mental practice and what we required the participants in the current experiment to do the current work—mental practice always involves rerunning a motor command that has already been established, whereas the participants in this study generated a completely new motor command and new phantom hardware with which to implement it. Although there is a great deal of literature that suggests mental practice improves performance, the consensus view is that it alters synaptic efficacy within established neural pathways (see ref. 23 for a landmark review on this topic). More recently, discovery of the mirror neuron system suggests that we have some capacity to activate motor preparatory systems on the basis of visual input, but there is no strong evidence that this extends beyond the exploitation of motor commands we have already established (see ref. 24 for a review, although see ref. 25 for evidence of motor facilitation during observation of biomechanically impossible finger movements).

That amputees can experience impossible movements of their phantom limb has been reported before—lower limb amputees have reported ''bending back'' their phantom shin to avoid contact with solid objects (26). The current results would suggest that such reports should also involve a change in the body image to allow such a movement to occur. Modifying the body image without first modifying the body has important implications, particularly in light of recent studies that demonstrate top-down effects of bodily awareness on the tissues of the body. For example, modifying bodily awareness via illusory ownership over an artificial limb—the so-called rubber hand illusion (7)—simultaneously induces a localized decrease in skin temperature in the ''disowned' limb'' (4). In fact, the current findings raise the possibility that the process of disownership of the previous phantom and subsequent reownership of the modified phantom, which was reported by the successful participants, would be accompanied by temperature fluctuations in the stump. Modifying bodily awareness by magnifying the appearance of a painful limb simultaneously increases the pain and swelling evoked by movement. Remarkably, minimizing the appearance of a painful limb decreases the pain and swelling evoked by movement (9). Those findings extend the possible effects of internally modified body image to top-down effects of body image on body tissues. This speculative, but not outrageous, proposition may have implications for our understanding and management of disorders characterized by disruption of body image and motor problems, for example motor neglect after stroke (27), back pain (28), and complex regional pain syndrome (29)—might the primary deficit underpinning motor difficulties in such groups involve the body image?

Crucially for this study, we corroborated participant reports with robust and established empirical methods. We used the intact hand as a control and participants cannot cheat on the left/right judgment task. Indeed, it is the accuracy with which response time data match patient reports that makes this finding dependable. Finally, although it remains to be determined whether or not a completely novel body image can be conjured via internal mechanisms in physically normal people, the current results show that the human brain can conjure completely novel representations via internally generated mechanisms, which has implications that extend across philosophy and the biological sciences.

Materials and Methods

Participants. Seven arm amputees (Table 1) participated in this study, which was approved by the institutional ethics committee and conformed to the Declaration of Helsinki. All participants reported a vivid sense of their phantom limb and preservation of willed movement of the phantom limb. None reported phantom pain or motor symptoms (for example clenched fist syndrome).

Training and Learning an Impossible Movement of the Phantom Limb. Participants were asked to spend 5 min every waking hour trying to move their phantom arm, from Position 1 to Position 2, the short, anatomically impossible, way. They were also asked to spend an equivalent amount of time imagining moving their intact hand in the same manner. Patients were phoned twice a week to encourage participation and an electronic diary was used to promote and record compliance (30).

Measures. ***Changes in body image.*** At the conclusion of the study period, participants were asked three questions: ''Did you learn the new movement?'', ''How did you go about learning the new movement?'', and ''Do you have anything else to tell us about your experience in this study?''.

Implicit motor imagery. A left/right hand judgment task (Recognize; NOI Group) was adapted for use with foot pedals (31). Left and right responses were indicated by depressing either the top or bottom (alternated between participants) of the foot contralateral to their amputation. Seven images of one hand were copied and flipped to produce 14 images and presented in random and counterbalanced order so that each image appeared twice per trial. Randomized trial conditions were: (*i*) palms down on the desk (control); (*ii*) hands held in Position 1 (Fig. 1*A*); (*iii*) hands held in Position 2 (Fig. 1*A*). Mean response time (RT) for correct responses in each of these conditions was analyzed. In this task, there is a tight coupling between RT and the distance one's own hand must travel to get from its resting position to the position shown in the picture. If less movement is required, then the response is quicker. If participants learned an impossible movement that substantially reduced the movement required, then RT for that image will decrease. RT in this left/right judgment task, therefore, obeys anatomical constraints (10). Participants were grouped as successful or not successful according to their report. We performed an ANOVA on reaction time data. There were two between-participant factors: side of amputation (left, right), and success (successful, not successful), and three within-participant factors: time (pretraining, posttraining); pictured limb (amputated or intact); and task posture (control, same as image, opposite to image). We analyzed reaction times for all images and also for only the two images that showed a hand in Position 1 or Position 2 (Fig. 1*A*). Significance was set at $\alpha = 0.05$.

Perceived motion path of a hand shown in alternating postures. We showed participants two alternating images of a hand (Fig. 1*B*). Flash rates ranged from 130 to 1,170 ms, at 80-ms intervals. Flash rate was randomized and counterbalanced so that each flash rate was used eight times. At each flash rate, the images were shown until the participant responded. We exploited the established phenomenon that healthy participants perceive the hand moving between the two positions through the long, physiological motion path if the flash rate is faster than the speed at which they can move their own hand between the two positions ($\approx$700–1,000 ms). When the flash rate is slower, healthy participants perceive the hand moving the short, impossible way (13). If participants learn to perform the impossible movement, they should always see the hands as moving the impossible way regardless of how quickly the images alternate.

Several methodological checks were undertaken after final assessment (*SI Text*).

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