NEUROSCIENCE

Probing the Neural Basis of Body Ownership

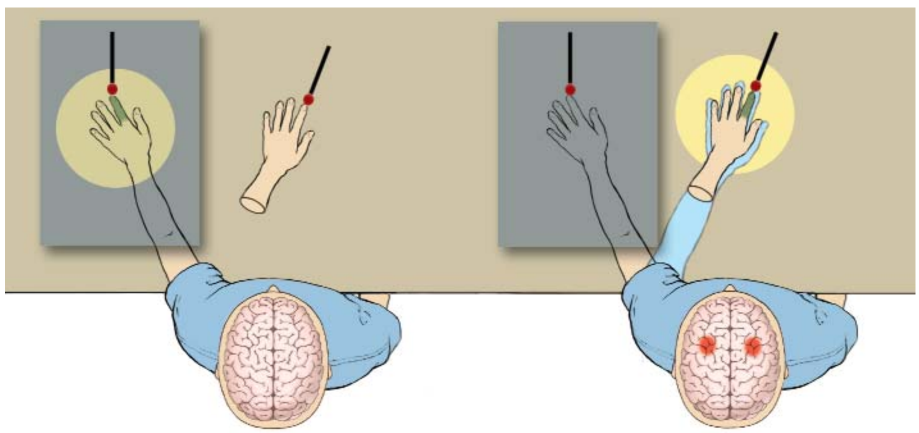
Matthew Botvinick

In the cognitive sciences, the most challenging phenomena are often the ones we take for granted in our everyday lives. An excellent example is body ownership. Ask any child whether his hands belong to him, and the answer is likely to be "Of course." But how do we distinguish our bodies, but not other objects, as belonging to ourselves, and what is the basis for the associated feeling of identification or ownership? The problem of the bodily self has long intrigued philosophers (*1*) and psychologists (*2*), yet only recently has it attracted the interest of neuroscientists. On page 875 of this issue, Ehrsson *et al.* (*3*) present an elegant functional neuroimaging study in which they probe the neural underpinnings of the bodily self.

An important idea underlying the Ehrsson study is that the body is distinguished from other objects by its involvement in the correlation or matching of special patterns of intersensory information. For example, there is a reliable correspondence between what our body position looks like and what it feels like. Visual input about body posture relates directly to information about proprioception, our intrinsic sense of position. Another important correspondence is between vision and touch—when we see an object contact our body surface, we anticipate a corresponding tactile sensation. Importantly, it is only the body, not other objects, that registers such intersensory correlations. Thus, the integration of visual, tactile, and proprioceptive information about the body can be thought of as self-specifying (*4*).

Evidence for a link between self-specifying intersensory correlations and bodily self-identification comes from diverse sources. Developmental psychologists, for example, have shown that the ability to register self-specifying correlations is present very early in life, alongside behaviors that appear to reflect self-recognition (such as touching one's face when looking into a mirror, after having had a mark unobtrusively placed on one's cheek) (*2*, *4*). Convergent evidence for a link between self-identification and intersensory correlations comes from a bizarre neurological syndrome known as somatoparaphrenia. In patients with this syndrome, damage to the right parietal lobe—a brain region that is crucial for intersensory integration—causes the individuals to deny ownership of their left arm or leg (*5*). The somatoparaphrenic patient may even insist that his own limb has been replaced by someone else's or that the limb is "fake" (*6*).

Surprisingly, just the opposite phenomenon can be induced in neurologically normal individuals, causing them to experience an artificial limb as if it were part of their own body. This is precisely what happens in the so-called "rubber hand illusion" (*7*). Here, the subject observes a facsimile of a human hand while one of his own hands is hidden from view (see the figure). Both the artificial hand and the subject's hand are then stroked, repeatedly and synchronously, with a probe. Under these conditions, the subject experiences an illusion in which the felt touch is brought into alignment with the seen touch, the way a ventriloquist's voice is brought together with the puppet's mouth. There is a compelling sense that one is feeling the probe as it touches the rubber hand, as if one is feeling "with" the rubber hand. Psychophysical experiments have shown that the rubber hand illusion is based on an overriding of proprioceptive input by visual information (*7*). However, the illusion involves not just a spatial realignment of the proprioceptive map onto the visual map, but also a feeling of ownership—subjects describing the illusion spontaneously report that the rubber hand feels as if it is "their hand."



This hand is my hand. Activation of the premotor cortex during the rubber hand illusion. In the illusion, normal individuals experience an artificial limb (rubber hand) as if it were part of their own body. (**Left**) The subject observes a facsimile of a human hand (the rubber hand) while one of his own hands is hidden from view (gray square). Both the artificial hand and the subject's hand are stroked, repeatedly and synchronously, with a probe. The green and yellow areas indicate the tactile and visual receptive fields, respectively, for neurons in the premotor cortex (red circles). (**Right**) The subject experiences an illusion in which the felt touch (green) is brought into alignment with the seen touch (illusory position of arm; blue). This brings the visual receptive field (yellow) into alignment with the rubber hand, resulting in activation of premotor cortex neurons.

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In their neuroimaging study, Ehrsson and co-workers investigated the pattern of brain activity that underlies this feeling of ownership. The researchers induced the rubber hand illusion while subjects underwent functional magnetic resonance imaging (fMRI). This revealed that the illusion is accompanied by activation of a frontal lobe region called the premotor cortex (see the figure). Control conditions indicated that this activation could not be attributed simply to viewing the rubber hand, or to seeing it touched. Furthermore, premotor cortex activation correlated with the strength of the illusion, and the timing of activation fit with the illusion's onset.

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Based on these observations, Ehrsson and colleagues conclude that "neural activity in the premotor cortex reflects the feeling of ownership of a seen hand" (*3*).

As the authors note, their findings square well with the idea that self-identification depends on the integration of multisensory information. The premotor cortex receives strong inputs from parietal regions that integrate visual, tactile, and proprioceptive information (*8*). In addition, animal studies have shown that the premotor cortex contains neurons with combined visual and tactile receptive fields. Interestingly, these visuo-tactile neurons appear to encode visual inputs by using a reference frame that is body-part centered (*9*)—that is, the cells respond both when a specific area of the body is touched, and when an object is seen approaching that same area. It seems plausible that such body-part–centered neurons might be directly responsible for the Ehrsson *et al*. findings. We know that, as part of the rubber hand illusion, proprioceptive information is distorted such that the position of one's own hand is remapped to the position of the viewed rubber hand (*7*). Presumably, when this happens, hand-centered visual receptive fields undergo the same shift, becoming aligned with the artificial hand (*10*). If this is the case, then viewing the probe as it approaches the rubber hand would activate hand-centered neurons in the premotor cortex (see the figure).

The foregoing account appears to explain why activation of the premotor cortex occurs during the illusion, but what does it tell us about the feeling of ownership? The intersensory matching theory seems to imply that this feeling is simply the subjective correlate of the neural events involved in registering self-specifying intersensory correlations. Understood in this way, the intersensory matching theory is, like other recent accounts of self-representation (*11*), quasi-reductive. The theory's claim is that, at the neural level, body ownership simply *is* the registration of self-specifying intersensory correlations. The fact that the relevant neural events correlate with the subjective experience of body ownership is critical to the theory, but the theory does not attempt to explain it.

The intersensory matching theory has an intuitive appeal, and the accumulated empirical data (including those of Ehrsson and colleagues) make it increasingly compelling. However, it also faces some interesting challenges. For example, if we accept that the activation of body-part–centered neurons is a hallmark of self-identification, then it should not be possible to observe such activation in the absence of ownership feelings. However, neurophysiological studies have shown that, during tool use, neurons with body-part–centered visual receptive fields (this time, neurons in the parietal lobe) are activated when objects approach not only the hand but the tool itself (*12*). From this finding, we would predict that tools are represented as belonging to the bodily self. However, although this may be true in some weak sense, the feeling of ownership that we have for our bodies clearly does not extend to, for example, the fork we use at dinner. Apparently, the activation of neurons with (usually) body-part–centered receptive fields may not be entirely sufficient to evoke a feeling of ownership.

Another issue facing the intersensory matching theory concerns the nature of the correlations involved. Although certain correlations can be understood as self-specifying, others appear similar in form but do not give rise to a feeling of ownership. For example, the rubber hand illusion can be considered analogous to the illusion of ventriloquism. Ventriloquism, too, is driven by familiar intersensory (visual-auditory) correlations (*13*). Yet this illusion has nothing to do with feelings of ownership. What makes the rubber hand illusion different? It is clear how self-specifying intersensory correlations might set our bodies apart from other objects, but what is it about these sensory maps that leads us to identify with our bodies, to link them with our sense of self? Perhaps the answer has to do with our ability to make our bodies move, and thus with our subjective sense of agency (*14*). Perhaps it has to do with specific relationships between interoceptive senses (such as proprioception) and exteroceptive ones (such as vision) (*4*).

Evaluating these possibilities and others pertaining to body ownership will require a willingness to engage phenomena that are, at least in part, irreducibly subjective. This willingness has been rare among experimentalists. The work of Ehrsson and colleagues provides an encouraging indication that this attitude may be changing, opening up fascinating new avenues of scientific inquiry.

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CHEMISTRY

The Modest Undressing of a Silicon Center

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The periodic table helps chemists systematize their thinking about the chemical reactivity of groups of elements on the basis of their valence. This approach is useful so long as one is aware of the "first-row anomaly" (*1*), which is mainly the result of the atomic orbital structure of these elements. In group 14, a large gap in physical properties and chemical behavior exists between carbon, the nonmetal of major importance to life, and silicon, the semimetal that drives the computer revolution. Among the most striking differences between these two elements is their opposite coordination behavior. Silicon has the propensity to form hypercoordinate (more than four neighbors) species (*2*), including heptacoordinate and even octacoordinate silicon complexes, which is not possible with carbon. Similarly, whereas carbon easily gives low-coordinate derivatives (tricoordinate and dicoordinate species such as alkenes and alkynes), which are the basic components of the synthetic chemist's toolbox, silicon rarely forms analogous species (*3*). Another important difference is the difficulty for silicon to maintain a bare positive charge, such as in R_3Si^+ (*4*), whereas numerous carbocations R_3C^+ are known to be stable (where R can be any of a wide range

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