Original Paper

We Three: My Brain, My Homunculus, and Me

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Abstract

An unconscious sense of the body in all higher mammals is located in somatosensory and motor cortices, colloquially referred to as the Homunculus (H). The time has arrived to consider how H might engage in the dimensions of selfhood that go beyond embodiment. Surely, the neural network modules that process various dimensions of selfhood must at least access and interact with the H or a stored memory of it. In this review, I suggest that our traditional understanding of H is much too simplistic. This review specifies a set of experimental approaches that should enlarge our understanding of the brain mechanisms of selfhood.

Keywords

Homunculus, consciousness, sense of self, somatosensory cortex, motor cortex

1. Introduction

The reference to *We Three* refers to the somatosensory and motor cortices and the unexplored possibility that these neural circuits integrate with other systems in the brain in the instantiation of the unconscious and conscious sense of selfhood. The focus necessarily revolves around cortical areas known in older literature as the Homunculus (H). Penfield first described H as a neural map model of body parts acting as a mechanistic system for registering which body parts are stimulated and which muscles are to be activated during movement (Weiss, 1988). I suggest that H is more than that.

Maps are useless unless something reads them. H maps are read by other neural circuitry that expands the repertoire of sensation and behavior. One could say that the self, unconscious or conscious, reads the body maps. What is this self and what contribution does H make to the construction of self-hood? Beyond the embodiment aspect of selfhood, H could be relevant to other dimensions of self-hood, such as body ownership (Low, 2003; Tsakiris, 2010), agency and willed behavior (Klemm, 2015), spatio-temporal location of selfhood (Aspell et al., 2012; Blanke, 2012), mirror neuron processes, introspective realization of ownership of thoughts and emotions, and abstract identity as a being

distinct from others. How could these dimensions of selfhood exist without reference to the body that manifests them?

While an unconscious sense of self obviously resides in those body maps, a question remains, as to how these maps might interact with other parts of brain in the conscious sense of self—the "I" to which each person lays claim. Even the brain areas mediating many unconscious thoughts and behavior likely interact with body maps.

Consciousness is a system property of brain that I propose here to use the body maps as a linchpin to stitch together the various needed network components. Surely, in order to mediate appropriate behavior, the neural network modules processing various dimensions of selfhood must at least access the H or a stored memory of it. To illustrate, it is the "I" of my brain who responds emotionally, cognitively, and behaviorally to the:

- Smells and sounds sizzling steak,
- Touch from others,
- Coldness of ice,
- Pain of a stubbed toe,
- Sound snap of a breaking bone,
- Sight of my missing limb,
- Sight of my body parts as I guide their movement, and, most significantly,
- Awareness that I am an agent engaging with the world around me.

In addition to shedding light on the nature of conscious sense of self, the experimental approaches proposed at the end of this review might advance our understanding of such phenomena as:

- Narcissism,
- The angst of anxiety and depression disorders,
- Illusions of phantom limbs and out-of-body experiences,
- Hallucinations of schizophrenia,
- Social withdrawal in autism,
- Lack of empathy in sociopaths,
- Loss of identity in such diseases as Alzheimer's and Capgras syndrome.

Additionally, the information might guide mental-health research and treatment.

2. Hypothesis

A popular view is that consciousness emerges from a coherent orchestrated function within a network of networks that inevitably includes body maps (Baars, 1983). We need to accommodate the role of H in the brain's basic organization as a network of interacting modules, with hubs that mediate functional connectivity among the modules. I propose that body maps are an integral part of network modules that construct the various dimensions of selfhood. Selfhood includes more than simple recognition of body

parts, but also the abstract "I" identity, subject/object distinction, location of self in time and space, ownership of thought and emotion, intentions, and agency. Even the sense of the metaphysical "I" is not so abstract as to be divorced from the body. After all, it is the bodily "I" that interacts with objects and others, navigates time and space, owns thought and emotions, and acts on intended behavior.

This hypothesis includes a possible role of H in the conscious awareness of selfhood dimensions. Mainstream literature on the bases of consciousness impute a role for body maps (D'Amasio, 2010; Thompson & Varela, 2001). See Figure 1 for a schema for these relationships. A recent review explores "embodied cognition", a concept similar to the one presented here that the brain's sense of embodiment could participate in perception, cognition, emotions, and agency (Cardona, 2017).
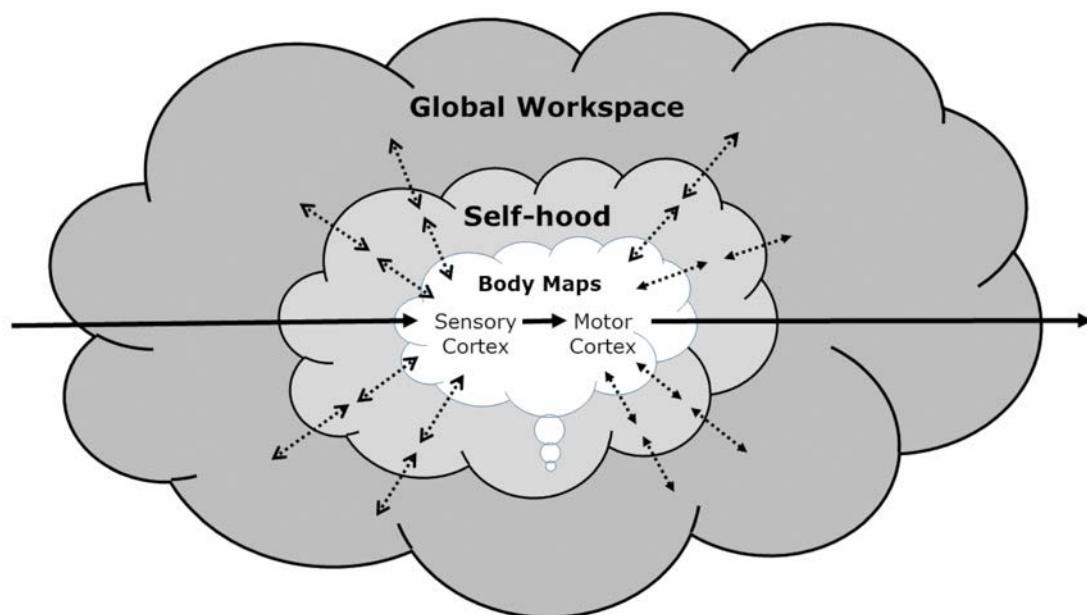

Figure 1. Diagram of the Hypothesis that Body Maps Are an Essential Part of the Brain's Representation of Self-Hood

The maps are embedded in a global workspace of general brain operations. Inputs to somatosensory cortex arrive not only from spinothalamic tracts but also from multiple regions of cortex and elsewhere; motor cortex receives input from cortical areas other than somatosensory cortex, and its outputs have well-known projections via the pyramidal tract and extrapyramidal routes to basal ganglia, brainstem nuclei, and cerebellum in the global workspace (see section, "Relevant Anatomy"). By "motor cortex" I mean not only M1 but also the premotor and supplementary motor cortices, which notably receive rich input from the posterior parietal association cortex and which have reciprocal connections with H's primary motor cortex (reviewed by Akkal et al., 2007; Hamadjida et al., 2016).

We can extend the thrust of Figure 1 by incorporating research on interacting brain modules (Huettel et al., 2004; Bassett & Sporns, 2017). For example, there are localized cortical circuits for somatic

sensation, movement control, mirror neurons, speech, sound, vision, facial recognition, and for executive control. H is surely one of the brain's modules, but its body maps likely lack sufficient mass of circuitry of their own to generate the multiple facets of a sense of personhood.

If body maps ae involved in ways other than embodiment as such, they may operate differentially in each selfhood dimension. For example, the cold winter day makes our whole body uncomfortable, a stubbed toe causes pain just in the affected toe, and the deliberate control of body parts varies depending on the situational context that prompts willed and controlled movement. Perhaps it is time for network models to have a hearing (Fig. 2).
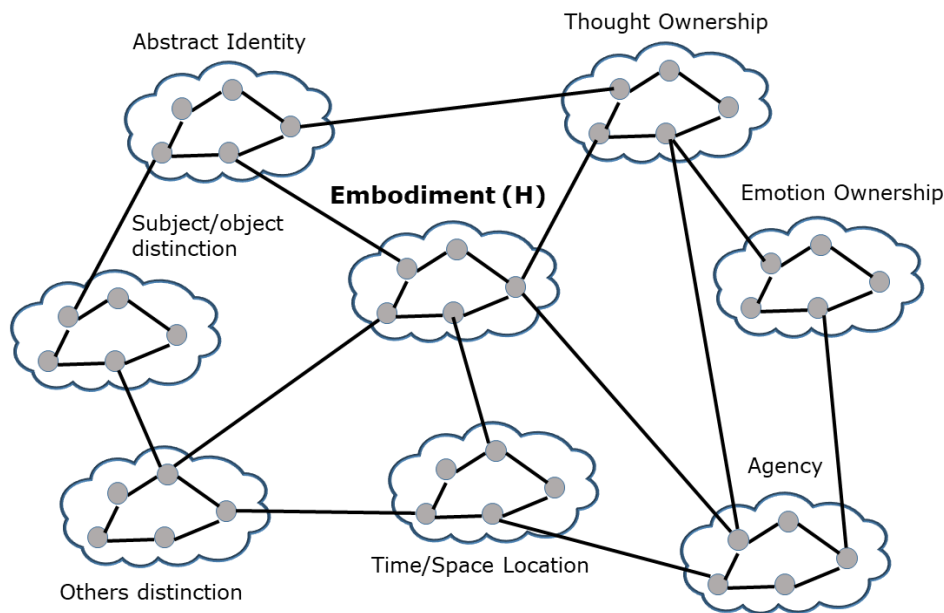

Figure 2. Putative Functional Connectivity of Modules Constituting the Network of Self-Hood

The brain areas performing a given selfhood module's functions are not entirely known. Interactions of the embodiment module (H) are suggested. The embodiment module depicts multiple nodes within it to reflect not only the distinctive sensory-motor functions, but also the mapping of multiple spinal segments. Which of these nodes connect to other modules under various circumstances remain undiscovered.

3. Rationale and Evidence for the Inseparability of H and Dimensions of Selfhood

Brains construct and interpret simulated mental models of reality. Our selfhood, whether explicitly perceived or not, is situated in those simulations.

Human sensorimotor cortex shows synchronous "resting state activity" in the brain's "Default Mental Network" (DMN) when the brain is not engaged in a task (Biswal et al., 1995). The hypothesis here predicts that DMN will change functional connectivity when the brain switches to tasks that engage the

various dimensions of self-hood. The nature of the change would likely vary with the specific nature of selfhood (embodiment, bodily location, ownership of thoughts and emotions, willed behavior and agency, and so on).

While direct evidence for the hypothesis is scant, sufficient support for this idea seems to justify experiments of the kind explained in the last section of this review. Support falls into two categories: psychophysical experience and functional neuroanatomy.

3.1 Psychophysical Experience

3.1.1 Multisensory Integration

All the senses have different processing zones in the brain. How do they get stitched together in creating the sense that it is "I" who simultaneously feels, sees, hears, smells, etc. or the "I" who intends, plans, and executes bodily movement?

Unisensory areas in somatosensory cortex process multisensory information by oscillatory entrainment of neuronal networks via direct cortico-cortical projections (Bieler, 2017). Note that this was one of the few studies to examine temporal distribution of impulses as it may relate to selfhood, a point revisited in the section here on Relevant Analytical Techniques.

One example of multi-sensory integration is that human intracerebral electrical responses to non-painful stimulation of median nerve spread from multiple somatosensory zones to motor cortex and multiple non-H neocortical areas and persist for some 200 msecs after stimulation ends (Avanzini et al., 2016). The hand region alone encompassed a widespread network covering more than 10% of the cortical surface of both hemispheres. An initial phasic component of the response occurred within primary somatosensory, motor, premotor, and inferior parietal regions, and additionally a tonic component lasting more than 200 msecs in opercular and insular areas.

Non-topographic sensory information affects how motor cortex modulates movement control in the context of personal and extrapersonal space (Serino et al., 2009). Mirror neurons provide another indication that body maps would be needed for "embodied simulation" that is required to mimic the behavior of others (Gallese, 2005).

Brain scans of arm-movement and grip-force manipulation clearly show increased activity in a large portions of H associated with the prediction of sensorimotor feedback from the efference copy of motor commands (Imamizu, 2010).

Another multi-sensory integration example is that during a hand-grasping task in monkeys, neurons in the motor cortex formed strong interconnections with premotor cortex and anterior inter-parietal cortex (Dann et al., 2016). Certain neurons had extensive connections with other neurons in the network, and their rhythmic activity at fixed frequencies seemed to coordinate information routing in the network.

Bodily posture processing requires multi-sensory integration. "Posture neurons" in the parietal cortex track egocentric body-part position via their reciprocal connections with motor cortex and somatosensory cortex and even parts of auditory and visual cortex. In rodents, about half of the parietal

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and motor cortex neurons are topographically tuned to postural features of head, neck, and back. Posture and body location in space are related by the connection between hippocampal place neurons and parietal cortex (reviewed by Chen, 2018).

Multisensory integration apparently even operates in such non-bodily selfhood functions as speech perception and language understanding. Transcranial magnetic stimulation and fMRI studies reveal that ventral motor and somatosensory areas of H participate (Schomers & Pulvermüller, 2016).

3.1.2 Higher-order Evaluation of Sensation

For example, in humans conscious selective attention regulates activity within somatosensory cortex and suppresses noise inputs (Iguchi et al., 2004). This is possible because somatosensory input is processed in multiple brain regions, not exclusively in the cortical sensory map.

Consider the subjective pain response to nociceptive stimuli. People vary widely in their subjective experience of pain, though they all presumably have the same H neural circuitry. The mental model the brain constructs for nociception must surely modify the interpretation of activity within H.

In the case of visual sensations, embodiment may seem relatively irrelevant. However, as visual input spreads into dorsal and ventral pathways of visual cortex, visual signals segregate to produce activity patterns that represent related features of visual stimuli (category, spatial location, color, texture, motion, etc.) (reviewed by Kosslyn & Koenig, 1992). Complete processing requires access to the body maps. For example, in the sub-network categorical processing of "What is it?" a look-up process will ascertain, "It is not me". In the coordinate subnetwork, look-up will ascertain "Where is it with respect to me?" The "me", of course, is found first in the body maps and then in whatever networks create the virtual "me".

Other features of conscious awareness would obviously involve other brain areas. Even though body-part representation is necessary, other brain areas likely interact with H to mediate functions such as ownership, valence, and salience of sensations, and planning of behavioral response. This necessarily engages multiple cortical networks that have reciprocal connections with the H. The egocentric meaning of such functions cannot be divorced from the body. It is "I" who see, hear, behave, etc.

3.1.3 Evaluation of Semantic Meaning

MRI mapping of semantic meaning shows that the meaning of most words activates more than one zone of neocortex, and H is richly engaged in processing meaning of hundreds of words that go far beyond simple embodiment. For example, almost all areas of somatosensory and motor cortex become active upon hearing a huge array of adjectives and nouns with diverse meanings involving abstract dimensions of personhood, cognition, and emotions (Huth et al., 2016). Notably less represented are words dealing with social interactions and time.

3.1.4 Self-consciousness

Self-consciousness entails a sense of body ownership, and this requires integration of sensory activity with activity in premotor and parietal cortex (Petkova et al., 2011; Ehrsson, 2012; Maselli & Slater, 2013; Blanke, 2012). Maselli's (2015) review of studies of self-location in full-body illusions suggests that body map neurons likely engage with multiple other brain areas (see below) to produce a cohesive combination of knowing one's body and knowing where it is.

Topographic mapping of body regions creates a template for matching and summating the map representations into a bodily whole (Petkova et al., 2011). This mapping allows creation of a single perceptual state that represents a first-order awareness of the body and perhaps its extended notion of self-hood. Once this first-order state exists, it can progress to a higher-order consciousness (HOT) (Carruthers, 2016).

Body movement commands require interaction with mapped sensory experience (Legrand & Ruby, 2009). Psychological studies are largely limited to body schema (Graziano & Botvinik, 2002), leaving a huge gap of possible H roles in emotion, cognition, and behavior.

In two brain-scan studies involving full-body illusions, sense of body location arises from a cognitive blend of egocentric body mapping with allocentric coding of the body's location (Maselli, 2015). Memory of where one has been located in space is tracked via the hippocampus, suggesting integrated activity between H and the hippocampus.

People who have out-of-body experiences retain their sense of selfhood (Blanke, 2012; Metzinger, 2004). Such experiences are rather common under influence of certain drugs (ketamine) or virtual reality illusions (Metzinger, 2004). In one of Metziner's illusions, he could see a 3-D image of himself standing in front of him, and if someone scratched his back, he felt the sensation happening to the body standing in front of him. Yet, despite this projection of selfhood, his selfhood remained trapped within its real skin. This suggests that H constrains reality to the actual body while at the same time having the capacity to contribute to a projected model of selfhood to the virtual image.

Self-hood-relevant affective consequences of somatosensory activation likely involve interaction between H and the limbic system. For example, brain functional imaging compared activity when a volunteer experienced pain and when told that a loved one who was in the same room was receiving a similar pain stimulus. The actual receipt of nociceptive stimulus to oneself activated sensorimotor cortex and posterior insula/secondary cortex, but the empathic response to the perceived loved one's pain was associated with bilateral activation in the anterior insula, anterior cingulate cortex, brainstem, and cerebellum. The authors concluded, "Only that part of the pain network associated with its affective qualities, but not its sensory qualities, mediates empathy".

3.1.5 Selfhood and Otherness

Body maps inform the brain there is a self that operates in a non-self external environment. For example, guiding movement of the body in relation to nearby objects requires integrating a neural

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representation of body schema and objects in the peri-personal space around the body (Holmes & Spence, 2004).

An example of the inseparability of H's role in self-hood and embodiment comes from the discovery of place cells in the hippocampus and grid cells of entorhinal cortex (Stensola & Moser, 2016). This spatial location system must include H in order to allow the brain to know where its body resides in space.

Self and "other" construction include one's own bodily mapping as the frame of reference. It is "I" who see you and references your bodily actions with respect to me and mine to yours. Mirror neurons, which mediate mimicking the movements of others, seem likely to have undiscovered connections with multiple areas of brain.

3.1.6 Selfhood and Executive Control

Motor cortex control of movement has numerous "upstream" influences from outside of H. This includes influence on motor cortex from auditory and visual inputs. Decisions may arise from competitive processes within H and its interacting without the need for an "I" authority figure (Miller, 2000). Perhaps such processing helps to create the illusion of an "I" controller.

3.1.7 Expression of Personality in Handwriting

The handwriting analysis community contributes to the rationale for this hypothesis. H directs the movements of handwriting, and yet handwriting is a rather specific indicator of one's personality and psychological state. Handwriting analysists claim that handwriting provides strong clues on people's states of mind, their character, temper, skills, emotions and even their physiology and brain health level. This would seem to be prima-facia evidence that multiple brain areas engage H, given that handwriting cannot be generated without engagement of both sensory and motor maps of hand and arm. Various kinds of brain damage and mental abnormalities produce distinctive changes in handwriting properties (Seifer, 2002). This should not be surprising, inasmuch as a review of 18 imaging studies indicated that handwriting activates widespread areas of frontal and parietal cortex and the cerebellum (Planton et al., 2013).

Recent neurological research demonstrates that the learning process of handwriting produces structural changes in the brain (James, 2019), improves the ability of children to generate written text (Jones & Christensen, 1990), affects word- and sentence-level working memory (Berniger et al., 2010), and builds a sense of writer identity and self-efficacy (Snyders, 2014).

One distinct way that non-H parts of brain affect handwriting is that visual illusions of hand ownership alter connectivity between H and inferior parietal cortex (Faivre et al., 2017). EEG gamma activity increased between left sensorimotor cortex and inferior parietal cortex during visual illusions of hand ownership. Subjective ownership correlated with the synchrony of somatosensory signals from the two hands. Hand ownership was stronger in subjects that had stronger alpha suppression over the sensorimotor cortex.

3.2 Functional Neuroanatomy

In all areas of neocortex, adjacent cortical columns link H to adjacent non-H areas by horizontal spread of axial dendrites at the pial surface and by intracortical project paths originating from pyramidal cells in cortical layers II and III.

The best known intra-map connection is the cross-hemispheric connection via the corpus callosum (Miller, 1975). The fiber tracts of the internal capsule provide multiple connections within and between each hemisphere and with the multiple circuits that contribute to conscious self-hood (Mountcastle, 1998).

Excitatory outputs from primary somatosensory cortex innervate widespread regions of motor cortex (Zarzecki, 1989). Apparently, we know much less about how different regions within each hemisphere's body maps communicate with each other. One study revealed that activity in one digit region of somatosensory cortex could inhibit the activity in another digit's field (Chowdhury & Rasmusson, 2003). One has to wonder about intra-H functions in the various dimensions of selfhood other than embodiment.

3.2.1 Somatosensory Inputs

The main sensory input to H comes mainly from spinothalamic tracts and thalamic VPL and VPM, but other inputs provide the brain with other kinds of information. For example, visual inputs do project to somatosensory mapped areas, in both mice and monkeys (Wang et al., 2012). Anatomical studies (Miller & Vogt, 1984) establish that areas 17, 18a, and 18b of rat visual cortex have connections with both sensory and motor cortex. Area 18a has reciprocal connections with sensory cortex. Motor areas have reciprocal connections with visual areas 17 and 18a and with many associational areas of cortex. Thus, cognitive, emotional, and behavioral responses to visual sensation do register in H.

Functional connections exist between body maps and both the insula and anterior cingulate cortex (Avanzini et al., 2016). Thus, a brain that has experienced somatosensory pain has learned to respond by activating affective components of pain, presumably by the inherent connections involving somatosensory maps, the pain network, and the limbic system.

Insular cortex is an integral component of the limbic system that seems to participate in several conscious selfhood-relevant functions, such as empathy, perception, motor control, self-awareness, cognitive functioning, and interpersonal experience. In the cat, the granular insular area projects to a constellation of somatosensory, motor, premotor and prefrontal districts. The dysgranular insular area links to lateral prefrontal and premotor, lateral somatosensory and perirhinal cortices (Clascá et al., 2000).

3.2.2 Somatosensory Outputs

Sensory inputs to somatosensory cortex spread to other non-mapped regions of cortex, and thus give H the connectivity needed to participate in various dimensions of selfhood beyond embodiment. For example, mapped snout inputs in pigs project into other non-mapped regions of cortex (Tanosaki et al.,

2014). The barrel cortex region of somatosensory cortex of rats sends outputs to other areas of the sensory map and also to diffuse long-range projections to primary auditory and visual cortex (Stehberg et al., 2014).

In rats, projections of somatosensory cortex modulate activity of innocuous and noxious inputs in the spinothalamic system (Monconduit et al., 2006). Glutaminergic activation of somatosensory cortical output enhances noxious-evoked responses, while $GABA_A$-mediated depression of corticofugal output suppresses noxious tactile-evoked responses of thalamic VPL cells. Given pain's dependency on consciousness, such results suggest that somatosensory cortex outputs may contribute to consciousness in general, not just to mapped perceptions.

Sensory cortex sends outputs to corticifugal neurons in motor cortex of cats (Zarecki, 1989). The primary sensory cortex connects with secondary sensory cortex and sends "massive" projections to the thalamus, brainstem, and spinal cord (Purves et al., 2017). Another example is that selective mapped responses to both tactile and nociceptive stimuli spread into other cortical areas, even in newborn babies (Verriotis et al., 2015).

3.2.3 Motor Cortex Inputs

Motor cortex has multiple inputs, especially from cerebellum, globus pallidus, and substantia nigra. A major source of input comes from premotor cortex, which in turn receives input from widespread areas of frontal cortex of monkeys (Muakkassa & Strick, 1979). In the macaque, motor cortex receives inputs from somatosensory cortex, parietal cortex, and thalamus, as well as inputs from premotor cortex (reviewed by Passingham, 1993). In the cat, input to motor cortex was identified by antidromic activation from cerebral peduncle, red nucleus, lateral reticular nucleus of medulla, or spinal cord. Recent studies of mice (Hooks et al., 2013) revealed long-range excitatory synaptic connections, particularly in upper layer pyramidal cells, from multiple cortical and thalamic areas.

3.2.4 Motor Cortex Outputs

Major outputs of motor cortex include not only the pyramidal tract, but also projections to the striatum, pallidum, and certain brainstem areas (subthalamus, red nucleus, substantia nigra) (Wise & Shadmehr, 2002). Given these multiple efferent projections of these areas, motor cortex must surely be central to multiple selfhood functions.

Chen et al. (2009) reviewed three fMRI studies showing neural interactions between auditory and motor areas during conscious perception of music. No doubt, this accounts for the toe-tapping response to strong rhythms.

4. Testing the Hypothesis

Research must move beyond reductionist methodology in order to understand the network dynamics that underlie higher brain functions of selfhood. The important research challenge is to develop suitable experimental approaches for assessing the coupling of H with diverse sensory, cognitive, emotional,

and motor modules. Tests should include specific tasks, motor planning, movement control, bodily misperceptions, and the effects after experimentally induced dysfunction. We need also to evaluate neural activity in H and related modules during various dimensions of self-hood along the sleep-wakefulness continuum.

4.1 Relevant Analytical Techniques

4.1.1 Magnetic Resonance Imaging

Brain scans, though increasingly popular, suffer the disadvantage that they measure metabolism, not signaling. Moreover, blood flow changes may occur upstream or downstream from the actual site of neurons that are changing their signaling activity. Magnitude of image changes is always small and subject to undue contamination by statistical noise and variability (Crew, 2016). Most importantly, it is likely that significant changes in nerve impulse patterns and connectivity timing can occur without requiring a change in over-all metabolism across a range of mental and behavioral states (Dubois, 2016).

Recording conditions typically require immobility, which limits the kinds of tasks that we can test. Subjects must have a high tolerance of claustrophobia, and the distractions of loud noise from the magnets inevitably affect brain function. Most imaging studies only report increases in activity, whereas decreases do occur and likely have major functional significance.

Activated areas often diminish as the subject rehearses and masters assigned tasks. Presumably, novel experiences require recruitment of more neural resources for processing than is needed after much practice and learning.

Nonetheless, the several MRI studies noted above support the proposed role of the body maps in conscious sense of self. MRI may indeed have sufficient sensitivity for certain functions, as indicated in hand-movement studies, by a high degree of temporal correlation within different regions of motor cortex and with time courses in several other motor-related areas (Biswal et al., 1995).

MRI scans might mislead us by false negatives. Also, scans would have little value if the switching between various cognitive states were short-term transients. In such cases, only unit activity or field potential measures would have the necessary temporal resolution. This fact gains standing in light of recent studies suggesting that consciousness operates in movie-like snapshots rather than as a continuous stream (Herzog et al., 2016).

4.1.2 Electrophysiological Methods

Electrophysiological measures include nerve action potentials and their proxy, the field potentials, as seen for example in the EEG. Unlike MRIs, electrical signals have fine time resolution, and with implanted electrodes, the spatial resolution limitations of field potentials may not be too limiting. The various frequency bands in field potentials are an especially useful metric (Buzsáki, 2006), because changes in conscious mentation are strongly associated with frequency-specific coherence changes, both cross-frequency and between various regions of neural networks.

An especially pertinent portion of the field potential frequency band is gamma activity, which is more prominent, relative to other frequencies, during wakefulness than during sleep or anesthesia. Especially worth investigating would be gamma coherence between H and non-mapped areas. Also in need of investigation are coherence measures between frequencies in the same areas.

Gamma activity from body maps may be relatively hard to detect because of the much larger amplitude of slower frequencies. High-frequency gamma waves are nested within and "ride on top of" irregular slow waves, persisting even in sleep states where the EEG is dominated by alpha and delta activity (Steriade et al., 1966a, 1966b). Perhaps a filtered EEG would be more sensitive for showing gamma activity changes in different cognitive states.

Frequency coherence can reflect any cognitive binding mechanism that varies with: 1) nature of cognitive task, 2) shifts long the sleep-wakefulness continuum, 3) body misperceptions, and 4) motor control and coordination. Synchronization may provide a way to generate the unity of conscious self-hood that normal people feel so intensely.

Synchronization occurs within single columns in separate columns in the same area of cortex and between columns in different intrahemispheric and transhemispheric areas. But I am not aware of studies of synchronization within cortical maps or between them and other areas of neocortex under task conditions.

Investigators are discovering great utility in the analysis of coherence of cross-frequency relationships. For example, a recent EEG study during an arithmetic task, rest, and breath focus, revealed that the proportion of epochs displaying a 2:1 harmonic relationship between peak alpha and theta frequencies was significantly higher when cognitive demands increased (Rodriguez-Larios & Alaerts, 2019). Opposite dynamics were identified for a specific range of "nonharmonic" alpha–theta cross-frequency relationships, which showed a higher incidence during rest compared with the arithmetic task. This kind of analysis could be useful for studying neural relationships in the context of various dimensions of self-hood.

Synchronization of scalp-derived has limited spatial resolution and is only useful for comparing different neocortical zones. We need data from implanted electrodes. If human neurosurgical patients are not available, it might be productive to evaluate the sensory and motor maps in a mammalian animal species that presumably has a degree of sentience.

Animal models make it more feasible to monitor actual signaling (action-potential trains) in defined circuitry. A common approach employs multi-unit activity, which is "noisy". One multi-unit attempt at dimensionality reduction of impulse discharges uses a two-stage process where spikes trains are smoothed over time and then a static dimensionality technique is applied to allow tracking neural trajectories over time. Such an approach has been used with monkey motor cortex to relate the spiking activity across a neural population to the monkey's behavior on a single-trial basis (Byron et al., 2009). For a given dimension of self-hood, the information content of a single spike train is not particularly

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meaningful, compared to the multiple spike trains in all the neurons in the network that processes that particular aspect of self-hood.

Investigators usually assume that the information content in spike trains resides in firing rate. However, there is clear evidence that individual neurons generate information also in the serial ordering of adjacent interval clusters, suggesting byte-processing (Klemm & Sherry, 1981; Sherry et al., 1982; Sherry & Klemm, 1984). I called such activity, "Circuit Impulse Patterns (CIPs)" and suggest that they are the fundamental representations of thought, emotions, and action (Klemm, 2011a). Unfortunately, to evaluate function in network modules in terms of interval coding requires sophisticated combinatorial statistical methods that do not yet exist. A complete understanding of impulse activity will require "revisiting" the role of body maps in terms of CIPs, not the usual methods involving fMRIs, field potentials, or even smoothed multi-unit firing rates.

4.2 Suggested Categories for Study of H-related Neural Activity

Either field potential or unit activity needs evaluation within H and between H and other networks under test conditions where the state of self-hood is selectively controlled.

4.2.1 Various Dimensions of Selfhood

The emotional dimension of selfhood provides rich opportunities for investigating H's possible role. The H is highly responsive to emotion-laden sensory input, such as the pain of stubbing a toe. Somatosensory zones do not scream for conscious attention when looking at a work of art. However, we are consciously aware that it is the "I" that is looking at the art, and we distinguish others who may be having their own view of the art. Perhaps our viewing launches a coherent co-activation of multiple zones in H or with visual and limbic networks. Nobody has tested such possibilities, though an approximation could be accomplished with experimental animals. The approach would be conceptually simple: implant electrodes in visual and limbic areas and an electrode array that spans several zones of somatosensory cortex. Then the field potentials at each electrode can be analyzed for frequency coherences while the animal attends an emotionally rich visual target. Using images of different salience and valence could disclose stimulus-specific coherence patterns that involve H.

Among the important variables to be evaluated is cognitive meaning of affective stimuli. For example, a touch can convey affection, clothing, or object contact (with different meanings depending on the object and situation). In response, muscle activation commands might indicate reflex aggression, affection, withdrawal, object manipulation, and so on. It seems likely that one could identify a role for H by constructing a topographic dictionary of the various physical and emotional conditions in which the sense of self participates. There might be value in evaluating activity in various states of consciousness.

Another variable is location in space, wherein: "I know where I am and where others are". A recent study advances understanding of self-location knowledge by recording the electrical activity of "place cells" in the hippocampus that fire impulses selectively when an animal is at certain locations within an

enclosure (Danjo et al., 2018). This study revealed that place cells not only coded self-location but also location of another rat in a T-maze. How does the hippocampus know it has a self to locate without direct connections with H? It seems likely that H is an integral part of an undiscovered larger circuit that communicates with hippocampal place cells in the construction of the virtual sense of self.

Also, how does the hippocampus know where the other rat is located? Well, of course, one rat can see or smell the other rat, but that information somehow has to get to the place cells. As far as I know, the connecting pathways have not been identified, except that there is a rather direct pathway from olfactory bulbs to the hippocampus. Rats may be like dogs; that is, to a dog another dog is a dog because it smells like a dog. The nose knows, and this includes self and other.

Activity patterns in body maps should likewise vary with the proximity of non-self targets in personal space. Electrical recordings would likely disclose which dimensions of self-hood are most heavily associated with body-map activity. Examples of manipulating states of self-hood could include the following:

- Embodiment: body awareness, various body positions or motions or the ways in which one perceives positions or motions.

- Body ownership: ownership perception with body-part illusions, proprioceptive manipulations, avatar projections.

- Spatio-temporal location: location learning testing, spatial skills tests, spatial illusions, elapsed time estimation, time illusions.

4.2.2 Task Specificity

Experiments should include monitoring brain activity during different kinds of tasks. It would likely be useful to examine functions comparing cognitive tasks that are abstract and impersonal versus those that require robust engagement of the "I". For example, function might be quite different when a subject looks at a drawing, makes a drawing, or imagines an original drawing. Other examples: compare activity when hearing a song, mentally constructing a melody, meditating without silent verbal chatter, and targeted verbal thinking. For motor functions, we might compare a well-learned simple pattern of finger tapping versus a complex and novel pattern of tapping. Other examples: having a finger or hand passively moved versus intentional movement or randomly scribbling versus writing words in elegant cursive or by printing.

It might also be useful to compare tasks that involved only a restricted portion of a body map. For example, we might compare electrographic patterns when viewing a scene versus viewing that scene in a computer game in which the subject controls specific body-part movement of an avatar. Other examples: tapping a pattern with one finger versus simultaneously tapping a different pattern with a finger on the opposite hand or pressing a button when seeing a cued visual target versus simultaneously pressing a button and tapping a foot and whistling.

4.2.3 Shifts Along the Sleep-wakefulness Continuum

H connectivity with multiple other cortical areas should vary at different points along the sleep-wakefulness continuum. We might predict that when the brain shifts from unconsciousness to consciousness, investigators will see unique connectivity shifts involving the body-map areas, both without and perhaps within the maps. Comparing responses to nociceptive stimuli is an obvious place to start.

Somatosensory areas likely possess neural correlates of varying states of consciousness (Koch et al., 2016). This supposition is readily testable by comparing neural correlates in sensory cortex areas when one is consciously aware of personal involvement in a situation and when one is not. Interestingly, one of Koch's hypotheses is that explicit representation of a stimulus requires an "essential node" of neurons that detect the feature without much processing. If so, body mapping could well be that essential node for conscious sense of self.

A common belief is that multiple modules operate in parallel and conduct much of their processing unconsciously (Dehaene & Naccache, 2001). In that view the brain becomes aware of this information consciously when there is top-down "attentional amplification" (and/or noise reduction) of the activity in certain of these modules that have become "coherent". When conscious attention engages H, the sense of self certainly becomes explicit and may amplify. How would that be reflected in H engagement with relevant brain areas?

Do body-map functions differ when one is conscious of personal engagement and when not? Differences surely occur at the level of motor function. As a player in a basketball game, I experience the conscious state of being in the game, but when shooting a free throw, I must selectively engage portions of my motor cortex in some of the planned movements. In both cases, how can I play the game without the conscious experience of my participation?

One rather obvious experiment could involve study of neural responses in mapped and non-mapped areas to a low-level stimulus of various body parts during various levels of wakefulness and attentiveness by the same subject. Of special interest would be such studies in patients who have deficient sense of ownership of certain body parts, as in the condition known as asomatognosia. For example, how would electrical responses compare when the patient is asleep versus awake?

4.2.4 Body Misperceptions

Bodily misperceptions in contrived laboratory experiments seem to occur without much engagement with body-map circuitry. However, these sensory manipulations are not the normal way humans locate their own body parts. The illusion research findings can result from a mismatch of conflicting senses. Moreover, these illusions do not trick everybody. Perhaps activity in H varies accordingly.

Bodily representation necessarily involves a wide range of sensory stimuli (visual, auditory, vestibular, and visceral) and motor signals and their feedback. A review of the existing literature indicates that bodily illusions arise because of misinterpretation of ambiguous or conflicting multisensory inputs

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(Aspell et al., 2012; Kilteni et al., 2015). These sensory inputs must surely register in somatosensory cortex.

4.2.5 Motor Control

Electrical recordings could elucidate the motor dimensions of H function as an animal mentally rehearses a complex series of movements it has been trained to perform or even suppress. For example, you could test for frequency coherences from an electrode array that spans several motor cortex zones and electrodes in other brain areas with functions relevant to the task.

Accurate goal-directed movement requires the brain's sense of self to assess a motor command in terms of targeting, sensor prediction, adaptation, and error correction. How can this not involve body maps?

A well-known phenomenon of motor control involves the idea that a motor command to muscles generates a feed-forward copy (efference copy), distributed to sensory cortex, as an internal model that is used to predict the anticipated sensory feedback and compared with the actual sensory feedback resulting from the movement (Von Holst & Mittelstaedt, 1950). Efferent motor signals and their feedback re-enter the brain by way of bodily mapped sensory receptors as an *afference* copy. Both sensory and motor bodily maps must inevitably be engaged in such a process, but this likely possibility has apparently not been studied extensively (Wolpert et al., 1995).

4.3 Experimentally Induced Dysfunction of Body Maps

It is not appropriate to produce lesions in the cortical maps of humans, though temporary effects of local anesthetics could be feasible. However, we can conduct psychophysiological evaluation of people with disease-caused damage, such as cardiovascular stroke. Such studies should extend beyond the usual evaluation of limb neglect.

However, stroke and other damage usually creates only partial loss of body sense. Transcranial Magnetic Stimulation (TMS) might provide a more complete and reversible inactivation of the cortical maps (Silvanto & Muggleton, 2008). Such experiments could allow selective assessment of the various sense-of-self dimensions. After TMS manipulation of H, investigators could ask subjects how they experience various cognitive situations and tasks.

5. Conclusion

Because H is one of the modules in the brain's global network, this review presents rationale, evidence, and suggested experiments for testing the proposed hypothesis that the H may likely participate differentially with other modules in the various dimensions of selfhood, not just embodiment. We can expect that interaction of mapped and non-mapped areas is task- and mental-state specific. Understanding these interactions could elucidate the mechanisms of consciousness.

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