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From multisensory integration in peripersonal space to bodily self-consciousness: from statistical regularities to statistical inference

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Integrating information across sensory systems is a critical step toward building a cohesive representation of the environment and one's body, and as illustrated by numerous illusions, scaffolds subjective experience of the world and self. In the last years, classic principles of multisensory integration elucidated in the subcortex have been translated into the language of statistical inference understood by the neocortical mantle. Most importantly, a mechanistic systems-level description of multisensory computations via probabilistic population coding and divisive normalization is actively being put forward. In parallel, by describing and understanding bodily illusions, researchers have suggested multisensory integration of bodily inputs within the peripersonal space as a key mechanism in bodily self-consciousness. Importantly, certain aspects of bodily self-consciousness, although still very much a minority, have been recently casted under the light of modern computational understandings of multisensory integration. In doing so, we argue, the field of bodily self-consciousness may borrow mechanistic descriptions regarding the neural implementation of inference computations outlined by the multisensory field. This computational approach, leveraged on the understanding of multisensory processes generally, promises to advance scientific comprehension regarding one of the most mysterious questions puzzling humankind, that is, how our brain creates the experience of a self in interaction with the environment.

Keywords: multisensory; bodily self-consciousness; causal inference; peripersonal space; computational model; virtual reality

Introduction and roadmap

An array of distinct energy signals exists in the world, such as electromagnetic radiations or pressure waves. A portion of these is then captured and translated by the peripheral nervous system, and eventually becomes objects of perception (e.g., sight, sound, and touch). Our experience of the world, nonetheless, is not fractioned according to the nature of energy signals or sensory modality, but instead we seamlessly integrate information from all sources into a coherent gestalt of the surrounding environment.[1–3] Indeed, via the process of multisensory integration, we are able to create a sensorial

unity guiding behavior and performance, mediating human–environment interactions.

Importantly, through the process of multisensory integration, it is not only the external environment and the body of the observer that is coalesced, but also the individual who perceives the external environment and the agent that executes actions on and in the world.[4,5] Namely, multisensory integration aids in shaping human–environment interactions on both the "environment" and "individual" side of the equation. Importantly, the individual or the subject is always linked to a body, that is, we experience the external world from a specific

location and with a specific perspective coinciding with that of a physical body, a body we feel as our own. Neuroscience research in the last 20 years has demonstrated that, although our bodies accompany us wherever we go, our sense of possessing and being encapsulated within a body is not inherent, but built upon sensory experiences, and in particular via multisensory integration. Indeed, while work by Stein and colleagues in the late 1980s and early 1990s established the modern era study of multisensory integration[6–10] (see below), Botvinick and Cohen in the late 1990s demonstrated via the rubber-hand illusion[11] (RHI; see below) that the sense of body ownership is not only malleable, but also dependent on the precise spatio-temporal characteristics of multisensory inputs.[12] This observation opened the possibility for empirical studies in the field of bodily self-consciousness, previously largely limited to theoretical investigations (although see Poetzl[13] and Gerstmann[14] for early neuropsychology evaluation of body-related disorders). Furthermore, this early work, linking the fields of multisensory integration and bodily self-consciousness, has permeated the design, implementation, and interpretation of much of the scientific inquiry within both fields. In fact, arguably, all illusions demonstrating the pliability of body ownership are rooted in the observation that sensory inputs presented in close spatial and temporal proximity are likely to be bound[15–18]—pillar principles of multisensory integration (see below for more detail).

Within this review, we first highlight the classical principles of multisensory integration as the starting point for both the study of multisensory integration and its sibling field of bodily self-consciousness. Then, we, respectively, detail the major advances within each field in the last decade. While the study of multisensory integration was arguably established in subcortex[1] (the superior colliculus (SC),[9,10,19–21] more precisely), a large portion of the modern day neuroscientific inquiry pertaining to multisensory integration has shifted to the cortex.[22–31] In doing so, the large amount of data collected in the late 1990s and summarized in "the principles of multisensory integration" have been translated into computational models bridging the gap between physiology and behavior[27,32,33] and providing novel insights into the mechanistic underpinning of multisensory integration. The field of bodily self-consciousness, on the other hand, has

taken a different direction. While neurocognitive models have been advanced in order to account for bodily self-consciousness,[4,5,34,35] these are by and large more conceptual than computational. Indeed, this empirical field of investigation being rather novel, the focus has been either experimental or philosophical. Departing from the classic principles of multisensory integration, this latter field has inquired how far can the boundaries of body representation be pushed, how may the body impact other areas of cognition (also for rehabilitation or wellbeing), and how utilizing multisensory principles jointly with novel technologies (virtual reality (VR) in particular) may impact society. Here, we argue that the current challenge for the field of bodily self-consciousness is to move beyond the classical principles of multisensory integration and instead translate the updated multisensory computational approach into a mechanistic understanding of processes leading to bodily self-consciousness. We propose that examination of the peripersonal space, that is, the space surrounding the body where bodily inputs are preferentially integrated by a well-studied population of multisensory neurons (see below), may be a particularly fruitful area of investigation pushing a computational understanding of bodily self-consciousness. This computationally oriented approach promises to advance the scientific understanding of one of the most mysterious and difficult questions of human kind, that is, how the brain creates the experience of a self in interaction with the environment via the body.

Multisensory integration

Classical physiological observations and principles

In the 1980s and throughout the 1990s, seminal recordings in the feline SC, a subcortical structure and critical node in the network mediating orienting behavior, arguably established the field of multisensory integration.[8–10,19–21,36–45] Namely, these recordings demonstrated the existence of neurons that not only responded indiscriminately to information from different senses, but also integrated this information and demonstrated neural gain. Importantly, the neural responses indexed were action potentials, and gain was measured as a deviation from linear summation. In other words, classic observations characterized audiovisual integration, for example, when the paired stimuli (i.e., AV) evoked a firing rate

not predicted by the sum of audio-alone and visual-alone discharges (i.e., A+V). Furthermore, supra-additivity (multisensory enhancement), in contrast to subadditivity (or even multisensory depression), was held as the gold standard to measure multisensory integration. These recordings and the characterization of multisensory responses laid out the governing rules of the named process; the so-called spatial, temporal, and inverse effectiveness principles of multisensory integration. The spatial and temporal principles, respectively, state that the closer in space or time two unisensory stimuli are from one another, the more readily they will be integrated or bound into a unitary multisensory percept. A third principle, of inverse effectiveness, states that multisensory gain is the greatest when unisensory stimuli evoke weak neural responses.

Additionally, the developmental trajectory and functional characterization governing multisensory integration was well established within the controlled walls of a laboratory setting. Indeed, based on electrophysiological evidence, it was argued that multisensory systems mold to one another to take into account the statistical regularities of the physical environment within which we live. More specifically, researchers observed that in the temporal domain, for instance, multisensory gain was the greatest when presentation of auditory and visual cues was offset in order to compensate for the differential times of transmission in medium (light being faster than sound) and neural transduction (the auditory system being faster than the visual one) of these modalities.[7,46–49] More causally, animals were reared whose sole sensory experience was that of synchronized audiovisual stimuli that were nonetheless spatially disparate by 18–30° of visual angle. These animals did not demonstrate the greatest multisensory gain when subsequent audiovisual stimuli were presented with no spatial disparity, as their control normal-reared counterparts did, but at a spatial offset corresponding to their rearing.[46]

Nevertheless, the brain is not composed solely of subcortical areas and it is unlikely that the process of multisensory integration that ultimately guides behavior is effectuated by single neurons. On the contrary, many of the actions that compose our daily lives necessitate background conditions supplied by the primitive brain, but are more closely associated with functioning of ensembles of neurons in the cortex. Furthermore, the world continuously

bombards us with noisy and ill-organized stimuli. During development, the brain is not sequentially exposed to a single multisensory pairing, but instead a number of objects are routinely present at once and events occur dynamically. In turn, the sensory signals emanating from a naturalistic environment ought to be causally segregated and integrated, and in a manner that permits the appropriate development of multisensory systems. That is, to successfully combine signals from different sensory modalities, the brain needs to detect which signals contain related information. Finally, we are not passive observers of events occurring in the outside world, rather we act upon the world to achieve specific behavioral goals, and in doing so, we further modify both the way our sensory systems operate (e.g., sampling different spatial locations or privileging specific sensory processes; i.e., active sensing) and the external world itself. Indeed, as multisensory inquiry moved from the feline SC to the primate cortex and incorporated more complex and ecologically valid scenarios, the principles of multisensory integration only appeared to apply moderately.[50–54] Furthermore, the focus shifted from explaining how single neurons integrate information to how populations of neurons effect this process[31,55] depending on the different behavioral needs an organism may encounter.

From principles to optimal models

Borrowing the observation from computational vision[56–58] that perception is inherently a stochastic inference problem, that is, the nervous system must deduce occurrences in an external environment it does not have access to, Ernst and Banks derived that when multiple and independent sources of sensory information are available, the optimal behavior—inasmuch as to increase accuracy and precision, and in the absence of a nonuniform prior—is to add sensory evidence linearly and weighted by the inverse of their variance (i.e., their reliability; see Fig. 1A).[59] Over about a decade, this maximum-likelihood estimation (MLE) model has been demonstrated to apply across the audio–visual,[60] visuo-tactile,[59] visuo-proprioceptive,[61,62] and visuo-vestibular[55,63–65] pairings, among others. More importantly, over the last half decade, the neural instantiation of this computational framework has been established.[27,55,66–68] Indeed, although the implementation of statistical inference,[69] or

A Maximum Likelihood Estimation
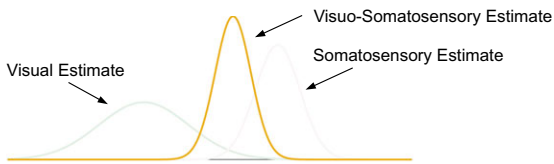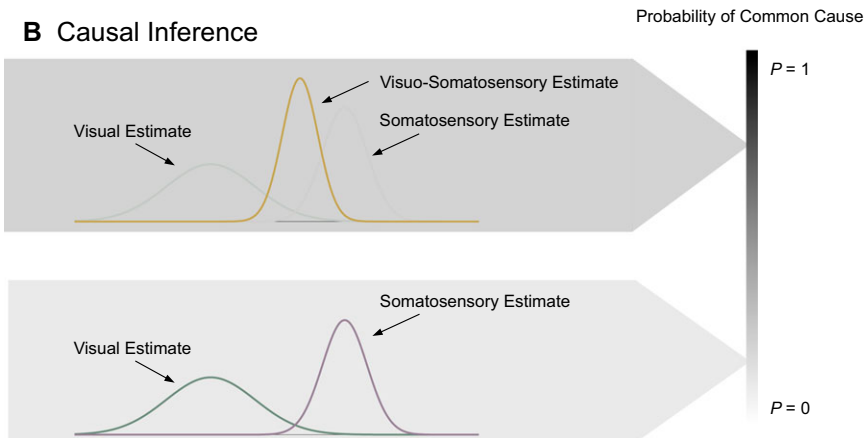

B Causal Inference

Figure 1. Maximum likelihood and causal inference models of multisensory integration. (A) In the maximum likelihood model, sensory stimuli are integrated into a single multisensory percept (visuo-somatosensory in this case, which is in dark yellow) from unisensory stimuli (in this example, visual and somatosensory, which are faded as they are not "experienced"). The multisensory percept has a smaller variance associated with it and is located in between the unisensory stimuli, according to the respective reliabilities of the unisensory stimuli; see Ernst and Banks[59] for equations). (B) The Bayesian casual inference (BCI) model incorporates a probability of common cause; where if a common cause is inference, MLE will proceed, but if the sensory stimuli are taken to emanate from distinct causes, instead of one integrated percept, two percepts each with their own likely location are computed. Accordingly, in addition to parameters similar to the MLE, in the BCI the perceiver has an additional latent variable—the prior for common cause. See Kording and colleagues for equations.[69]

inference based on probability distribution, in the noisy devices that are neurons may appear an impossible task, in a hallmark theoretical study Ma and colleagues suggested that it is precisely because of the inherent variance in neural firing that MLE may be performed within the brain.[33] This so-called probabilistic population coding (PPC) framework states that as neural discharges are Poisson distributed, that is, their variance scales positively with the rate of neural firing, when the firing rate of a population of neurons is plotted as a function of their preferred stimuli, this population activity takes on a noisy Gaussian shape. Furthermore, when two such populations (e.g., auditory and visual) converge downstream onto a multisensory set of neurons (e.g.,

audiovisual), these form a "hill" of activity that is shifted correspondingly to their relative variances, just as in MLE (Fig. 1A). In other words, the PPC formalizes that while the MLE mathematically requires multiplication (i.e., estimate from one signal multiplied by its weight given its reliability added to the weighted estimate from the other modality), this operation may be accomplished via linear summation of neural codes. Thus, the PPC shifts the burden of multisensory integration from single neurons to populations of neurons.

Given this theoretical framework, Angelaki and colleagues recorded from dorsal medial superior temporal (MSTd) neurons while presenting monkeys with visuo-vestibular stimuli.[55] Importantly,

the stimuli conveyed motion and covered the entire state-space, that is, 360°. Furthermore, visual motion coherence was parametrically manipulated. The authors sought to determine whether as predicted by the PPC, a linear sum of activity derived from unisensory conditions could account for spiking activity engendered during multisensory presentations. And while findings from these recordings revealed that a linear summation could account for the data, this summation required weights that were not always equal to "1," and more vexingly, these weights were altered by visual motion coherence.[55] This finding has been replicated a number of times,[31] and the functional significance of MSTd neurons firing and their weights altering with cue reliability has been demonstrated in heading behavior.[67,70,71] Thus, while the PPC predicted that neural weights equal to 1 (i.e., simple linear summation) would account for statistical inference due to the stochastic firing of neurons themselves and the fact that they have "preferred" stimuli, neural recordings demonstrated that neural weights were not equal to "1" (i.e., simple summation) and varied with the nature of sensory stimulation. In turn, an explanation for shifting neural weights was required. Ohshiro *et al.*[72] proposed that divisive normalization, a prevalent neural operation normalizing the contribution of each individual neuron to a downstream target by the summed activity of a population of neurons, at the level of multisensory integration could account for the fluctuations in neural weights as a consequence of cue reliability. Indeed, the intuition is that altering visual motion coherence will influence the output from visual neurons, whereas vestibular neurons will not change their firing rate as a function of visual coherence. Hence, when adding these two populations, the summed activity takes on drastically different values as a function of visual coherence, but also whether only visual or vestibular outputs are included in the divisive pool, or whether the visuo-vestibular neurons are also included. That is, vestibular neurons may contribute to activity of the divisive pool of neurons, but this is not influenced by visual coherence, and hence minimizes the impact of coherence in the multisensory condition, in contrast to the visual condition. Elegantly, this theoretical postulation may equally account for classical observations in subcortical multisensory physiology, such as the

spatial or inverse effectiveness principles of multisensory integration.[72] In fact, as unisensory stimuli evoke stronger and stronger responses, the overall activity of the divisive pool also increases, and hence multisensory gain decreases—as described by the principle of inverse effectiveness (see Ohshiro *et al.*[72] for more detail). Lastly, the divisive normalization interpretation brings forward a critical prediction; namely, that a nonoptimal stimulus for one modality which activates a neuron when presented in isolation should be able to suppress the response to a near-optimal stimulus of the other modality when the cues are combined. Recordings in MSTd have recently confirmed this prediction,[24] further highlighting populations of neurons as machines of (multisensory) statistical inference.

A modeled measure of the environment and brain

While the MLE framework is able to account for a host of psychophysical findings, and as illustrated above its neural implementation is every day further comprehended, it is far from a complete model. Most notoriously, the MLE is a so-called "forced-fusion" model, in that it does not solve the correspondence problem.[73,74] In other words, even when multiple sources veritably originate from different causes and thus ought not to be integrated, the MLE framework will predict that the compound sensory signal emanates from a single source placed somewhere in between the two real sources. This is because the MLE does not incorporate priors (or has a uniform one). For example, in the case of a ventriloquist moving a puppet's mouth, we all have the experience of attributing the heard voice to the puppet. However, the MLE would predict that in the case of similar sensory reliabilities, we would locate the origin of our audiovisual experience to somewhere in between the puppet and the ventriloquist. A successful approach in dealing with this limitation is the addition of priors, or expectations, to the model. For instance, in the case of the ventriloquist example, we expect voices to emanate from moving mouths, and hence we attribute the voice to the puppet and are prone to the illusion even when auditory information clearly emanates from the (unskillful) ventriloquist. In other words, the addition of priors, such as a coupling or common source prior in Bayesian models[69,75–80] allows for greater flexibility; weighting sensory evidence (i.e.,

likelihoods) with expectations or priors. An example of a Bayesian model incorporating a prior—a common cause prior in this case—is the Bayesian causal inference (BCI)[69] model, where when a common cause to sensory signals is inferred MLE is performed, and when distinct causes are most likely, integration does not occur.

In more detail, the BCI model is a class of Bayesian model—in that sensory likelihoods are combined with a prior—which makes an inference about the causal structure of events in the environment (one versus two causes) given the spatio-temporal locations and reliabilities of sensory stimuli and a prior probability of attributing a common (singular) cause (see Fig. 1B and Kording *et al.*[69] and Samad *et al.*[81] for more detail). This model is able to account for an array of psychophysical findings—including those detailed by the MLE. Importantly, Bayesian models inherently adapt to and allow for a dynamic world in which sensory expectations are updated given sensory history.[82,83] Thus, under a framework incorporating priors, multisensory brain circuits are able to learn new statistical regularities through behavior. Furthermore, back fitting data to these models allows extrapolating latent variables, such as the prior probability of attributing common cause to multisensory signals given certain stimuli properties, not directly measurable in the brain or through behavior without a model (see Ref. 84). Interestingly, recent work has combined a modeling approach incorporating Bayesian priors with direct auditory recordings of the environment to suggest that, in fact, as suggested by early physiological recordings, the nervous system adapts (developmentally, but inclusively evolutionarily) to the statistical regularities of the external world.[85] Ernst and colleagues were able to illustrate this occurrence both within, and importantly, beyond the limits of the laboratory setting. More in detail, cross-modal correspondences such as that high-frequency sounds emanate from elevated visuo-spatial locations are commonplace.[86] Hence, these researchers queried whether such correspondence is reflected in the natural statistical of the environment. Their findings demonstrated that, indeed, in the external environment high-frequency sounds tend to originate from higher elevation, and further, that head-related transfer functions dictated by pinna shape tend to accentuate the bifurcation of higher and lower frequency sounds in elevation (see Burge

and Geisler,[87] for a similar demonstration in the visual domain).[85] Most strikingly, in an auditory localization task, human participants demonstrated clear frequency biases, and these biases were well accounted by priors mimicking sound frequency-location patterns present in the environment and the filtering properties of the ear.[85] This study, hence, is a perfect example of the translation from classical principles (i.e., multisensory systems mold to the statistical regularities of their world) to real-life demonstration, based on the use of computational models.

A current limitation of Bayesian models, however, is a profound lack in understanding their neural instantiation, in particular from a physiological perspective or even a biological plausibility standpoint, (although novel neural network modeling is rapidly narrowing this gap in knowledge[88]). Importantly, the fact that Bayesian models may account for findings including and surpassing those detailed by the MLE, yet this latter approach and not the former is firmly grounded in the brain, should not be a deterrent, but an incentive for future research. In fact, recent sophisticated functional magnetic resonance imaging (fMRI) work has suggested that distinct computational principles may govern multisensory integration across the neocortical mantle. More precisely, Rohe and Noppeney[89,90] employed an audio-visual localization task in conjunction with an fMRI multivariate pattern analysis approach to study how unisensory and multisensory processing are instantiated in primary auditory and visual areas, as well as in multisensory parietal areas. Results suggested that while in auditory and visual areas neural decoding was most correlated with segregated estimates of stimuli location for each modality, in the posterior intraparietal sulcus (IPS), the location of stimuli was estimated under the assumption of unity (e.g., MLE), and only in the anterior IPS was the uncertainty about the causal structure of the world taken into account and sensory signals were combined as predicted by BCI (see Boyle *et al.*[91] for a similar analysis and interpretation of electroencephalography (EEG) data). Hence, while recent work by Angelaki and colleagues[27] has elucidated how action potentials originating from an ensemble of neurons may perform MLE, Noppeney and colleagues[89,90] have suggested (via an indirect measure such as the blood oxygen level-dependent (BOLD) response) that unisensory estimates,

MLE, and BCI may coexist in the brain. Future physiological work ought to focus on translating the above-mentioned BOLD findings into the language of neural impulses, and detailing the computations involved in transitioning from MLE (in the posterior IPS) to BCI (in the anterior IPS) and models incorporating Bayesian priors more broadly. More generally, a unified theory of multisensory integration, encompassing a solution to the correspondence problem (i.e., allocating signals to sources), the binding problem (i.e., appropriately integrating and segregating sources given signal properties), and the reference frame problem (i.e., from eye- to head- to limb-centered representations), awaits, but advances. Indeed, an interesting candidate is that of correlation detection.[92] By using an architecture similar to that of the Hassenstein–Reichardt detector,[93] Parise and Ernst[94] have recently detailed a model solving the correspondence and integration problems. More specifically, this model uses a series of low-pass filters and simple mathematical operations (summation, multiplication, and convolution) to resolve the correspondence problem, and then pools across spatially aligned multisensory correlation detectors in order to perform MLE. Interestingly, this last step in the model involves a divisive normalization step, reminiscent of physiological work postulating this same mechanism as culprit in neural reweighting as a function of stimuli reliability.[24,72]

Bodily self-consciousness

In order to understand human–environment interactions, we need to explain not only how external stimuli are processed, but also how they are associated with the perceiver, or the subject of experience. Critically, the perceiver is linked to its physical body. Indeed, the body is the sole entity always present in every single experience, and it is the location from which the world is perceived and acted on. In fact, it may be argued that any experience of the external world ought to rely on a multisensory bodily representation of the entity to be subject of the experience; a process globally denominated bodily self-consciousness. Interestingly, the body is a very particular multisensory object, as in addition to receiving information from exteroceptive objects, it is also continuously bombarded by proprioceptive, vestibular, and interoceptive signals

that are omnipresent. Hence, just as with the representation of the world at large, the scaffolding of bodily self-consciousness is rooted in the process of multisensory integration.

Studies that have carefully manipulated properties of the multisensory environment have demonstrated that bodily self-consciousness is not inherent, but built based on multisensory stimuli[4] (see below). Indeed, the general consensus is that although the specific sensory inputs that the body receives may vary, this input overwhelmingly abides by the spatio-temporal principles of multisensory integration.[35,95–97] In turn, our sensory history is stacked with evidence indicating that when a sensorimotor command is made to perform an action, and as a consequence a particular object that looks like my hand approaches and makes contact with the target of that action, I eventually feel touch at the location of visual contact. The most parsimonious explanation to the confluence of spatio-temporally congruent sensorimotor, visual, auditory, tactile, proprioceptive, and vestibular information (among others) must be that all these sources of information relate to the same entity, my body. Critically, bodily illusions (such as in the RHI[11]) nicely illustrate that introducing multisensory conflicts can easily alter bodily ownership, as we will review in the next paragraphs.

As we put forward in the rest of this section, an array of bodily illusions—all dependent on classical principles of multisensory integration[3–16]—has been described and utilized to scrutinize the neurobiological underpinning of bodily self-consciousness. Furthermore, more recently, these illusions, because of their impact of bodily self-consciousness, have been used to demonstrate the link between the latter and other aspects of perception and cognition.[98,99] Indeed, as we highlight below, a major novel area of inquiry relates to the plasticity of bodily self-consciousness and leverages this feature in social cognition.[100] Lastly, conceptual models accounting for the sense of body ownership have been proposed and numerous neuroimaging studies have delineated the brain areas involved in the process.[101] However, computational models bridging between physiology and behavior are lacking. In fact, we propose that just as the study of bodily self-consciousness was jumpstarted by borrowing principles from multisensory integration, it

is now time to adopt the more recent computational principles established in the latter field.

Classic observations and neurocognitive models

Nascent from the demonstration that tactile stimulation on a participant's hand as well as synchronous (as opposed to an asynchronous control) visual stimulation on a laterally displaced rubber hand may induce the sensation of ownership over the fake hand (i.e., the RHI),[11] and inclusively alter the discharge pattern of neurons encoding for the position of the limb in space,[102] researchers have tirelessly probed the limits of limb ownership.[12,103–112] More broadly, researchers have demonstrated that it is not only fake limbs that may be artificially embodied, but also faces,[15] the tongue,[113] legs,[114] feet,[115] and whole bodies.[17,18,116,117] Via the use of VR, participants may be fed with an online video recording of their body positioned a couple meters in front[18] or behind[17] them. Then, when synchronous (as contrasted to asynchronous) visuo-tactile stimulation is administered, participants report feeling ownership over the virtual avatar and to self-locate at its position. It is important to highlight that although this latter finding may superficially appear nearly identical to the RHI, there is a fundamental conceptual difference (in addition to empirical distinctions). Namely, humans do not consider a particular limb to enclose their self. Contrarily, in the latter case of the full body illusion (FBI), it is not a particular limb that drifts toward a disembodied location, but instead their whole persona is shifted in space and is identified with the virtual body. That is, the proprioceptive bias induced in the RHI may be considered from an egocentric perspective (i.e., "my hand is further leftward in the synchronous than asynchronous condition"), while variations in self-location provoked by the FBI may solely be considered from an allocentric or spatiotopic perspective (i.e., "I am closer to the location of the virtual body in the synchronous than in the asynchronous condition"). In other words, while body(-part) ownership is altered in the RHI, both self-identification and self-location are altered in the FBI. For completeness, the RHI and FBI are not only dissimilar from a conceptual point of view, but also from an empirical one—the RHI for instance is limited to a real hand to fake hand range of about 30 cm,[110] while no finite range is known for the FBI. Similarly, while

the vestibular system is an important component in bodily self-consciousness (a sensory modality that is by default "global"),[118–120] this sensory modality does not appear to strongly contribute to the RHI (but see Refs. 121 and 122), which instead importantly involves proprioceptive inputs.

In addition to detailing experimental manipulations limiting or reinforcing the RHI, a number of researchers have postulated neurocognitive models in search for a mechanistic explanation. In their initial illustration, Botvinick and Cohen[11] simply proposed that the RHI arises from the interplay between vision, touch, and proprioception, suggesting the seminal idea that the higher spatial resolution of the visual system would induce a visual caption of touch. This intuition was better detailed in Makin and colleagues' proposal that visual and proprioceptive cues about the positions of the real and rubber hands are first combined into a single estimate of the hand's spatial configuration.[96] It is only subsequently that tactile information is combined with the spatial estimate of the hand, and if successfully integrated, elicits the RHI. Indeed, based on a series of neuroimaging studies,[101,123,124] it has been speculated that tactile and visual bodily inputs are first processed in somatosensory areas and inferior temporal extrastriate visual areas (e.g., the extrastriate body area[125]), these inputs then converge and are integrated in posterior parietal (and likely ventral premotor) regions,[123] and finally the recalibration of proprioceptive coordinates occurs in the IPS.[5] Yet, other experimental findings indicate a contribution of structural information and congruency effects in determining the RHI. That is, body ownership is reduced if a nonhand shaped object is shown or the rubber hand is placed in an anatomically impossible body posture. In turn, according to a recent neurocognitive model, the integration of multisensory cues is gated by a pre-existing internal model of the human body and its structural features (e.g., shape and anatomical plausibility of body parts configuration). In this latter account, Tsakiris[34,97] proposed that a "test-for-fit" process takes place via neural processing in the right temporo-parietal junction, to determine whether an external object can or cannot be embodied accordingly to structural features. Furthering the description of an "internal model of the human body," and finding inspiration in the broader predictive coding framework, it has most recently been proposed that the RHI results from

minimizing the prediction errors that arise from feeling tactile sensation on the real hand and seeing the touch on the rubber hand.[126,127] Error minimization would thus result in merging the spatial representations of the two hands and, putatively, updating beliefs (i.e., priors) about one's own hand location and appearance.

Now, despite the insights that these neurocognitive models provide about plausible neurobiological mechanisms underlying limb-ownership, to date the vast majority of these proposals have been formulated at a conceptual level, without addressing the underlying computational problem (see Samad *et al.*[81] and discussion of this report below for a normative approach to the RHI). In addition, as abovementioned, limb-ownership is merely a component of bodily self-consciousness; the self-being encapsulated within the body as a whole, and not a single limb. Hence, neurocognitive models detailing the processes necessary for the RHI do not account for global aspects of bodily self-consciousness. A normative approach encompassing both limb- and whole-body embodiment is required. Indeed, Samad *et al.*[81] provide a normative model of the RHI by casting visuo-proprioceptive coupling in light of BCI and observing that the illusion results when a single cause (as opposed to two) is inferred; however, this initial model does not account for embodiment as a whole (versus body-part embodiment) and cannot account for the subjective experience of the self-being relocated during the FBI or for the possession a first-person perspective. For instance, an account incorporating not only how visuo-proprioceptive signals shape arm ownership,[81] but also how the vestibular system impacts global aspects of embodiment and interacts with body-part specific representations (i.e., integrates with proprioceptive signals) is lacking. This particular research program—querying the integration of local and global aspects of bodily self-consciousness via the study of visuo-vestibular and/or vestibulo-proprioceptive integration may be particularly fruitful in light of our deep understanding of the neurobiological underpinning of visuo-vestibular integration (see above[27,55]). In this context, searching for a global account of bodily self-consciousness, Blanke and Metzinger[128] first outlined the three necessary components for minimal self-hood; body ownership at the level of the whole body (i.e., self-identifying with a body), self-location (i.e., experience of where "I" am in space), and a first-person perspective (i.e., from where "I" perceive the world). Next, via myriad empirical observations,[4,18,35,119,129–134] bodily self-consciousness and the named components were firmly rooted in the brain and scaffolded on the process of multisensory integration. Finally, a set of constraints for bodily self-consciousness has been delineated.[35] More specifically, it has recently been proposed that for multisensory inputs to lead to full-fledged bodily self-consciousness, they must fit within the proprioceptive, body-related visual information, embodiment, and peri-personal space (PPS) constraints (see Ref. 35 for detail).

In sum, it is now taken that bodily self-consciousness is composed of a number of phenomena (ownership and self-location, among others), and that these components are rooted in the process of multisensory integration.[4,5,35,128] While a first normative computational model of the RHI does exist,[81] an explicit neural, computational, and mechanistic account of full-fledged bodily self-consciousness is still lacking. In the next section, we focus on recent empirical observations relating to the PPS constraint of bodily self-consciousness in an effort to sketch how these findings hint toward a viable approach aiming for a mechanistic understanding of bodily self-consciousness. More precisely, the PPS constraint specifies that body signals occur within the limited space surrounding the body—the PPS[135–138]—and hence for signals to bind with body-related information they must occur within this space. In this line, recent work has depicted a more complete picture regarding the encoding and functional role of the PPS, and has revealed the stochastic and predictive[139–141] nature of this particular form of spatial representation critical for bodily self-consciousness. Thus, we propose that by highlighting the stochastic or statistical inference nature of PPS representation, as one fundamental component of bodily self-consciousness, it may be possible to leverage recent advances in computational models dedicated to multisensory integration in the study of bodily self-consciousness.

A stochastic body space

The PPS is the space immediately adjacent to and surrounding an organism's body.[22,142–144] It is encoded by multisensory neurons within a fronto-parietal network, possessing somatosensory

receptive fields on a given body part, as well as depth-restricted auditory[145] or visual[146] receptive fields. Importantly, these exteroceptive receptive fields are anchored on the given body-part, and hence encode auditory or visual information in a body-part centered reference frame, and only when objects or events occur near from the body. Furthermore, electrical stimulation of fronto-parietal neurons with multisensory depth restricted receptive fields elicits highly stereotyped defensive-like movements, such as ducking or deflection of incoming stimuli.[147,148] Given these empirical findings, it was suggested that the PPS, or more precisely, the depth-restricted receptive fields of multisensory neurons constitute an interface for body–environment interactions,[149] by detecting potential contacts with external stimuli and triggering adequate defensive or approaching behaviors. This space has been documented around different body parts, most notoriously the hands,[150] but in recent years equally the face[151–153] and trunk.[154–159] Furthermore, while the original neural description of the PPS was undertaken at the single cell level in nonhuman primates,[160–163] in later years a similar encoding has been inferred in humans first via neuropsychology[135,143,164] and then neuroimaging[22,124,165] and psychophysics.[158,166–169] Psychophysically, the PPS has been widely indexed by applying tactile stimulation on the body and asking participants to react as fast as possible to this stimulation while either auditory or visual stimuli approach the body.[142–170] Results demonstrate a multisensory facilitation effect (i.e., reaction times to audio-tactile or visuo-tactile stimuli being faster than to tactile stimulation alone) that is spatially dependent; when audio–tactile/visuo-tactile stimuli are in proximity, but not when they are far away. In other words, PPS seemingly obeys the spatial principle of multisensory integration (see Serino *et al.*[171] for review).

Most significantly for the current purposes, empirical findings have suggested that the PPS is an important contributor scaffolding bodily self-consciousness. That is, not only is there a strong correspondence between the size of peri-hand space and the spatial extent over which the RHI is possible,[81,110] but more importantly, when participants are submitted to the FBI, their PPS translates in space toward the virtual body for which the illusion is induced, as to encode the perceived location of the self in space and not the physical location of

their body.[155] More specifically, when participants see a virtual rendering of their physical body placed 2 m in front of them, and this virtual avatar is stroked in synchrony with touch they feel in their body, participants feel as if they drift toward the virtual avatar. In correspondence, their audio-tactile peri-trunk space (a representation that has been argued to delineate the whole body PPS[156]) expands in the front space and shrinks in the back space, as if globally translating toward the virtual avatar.[155] Intriguingly, this effect is present even when participants are not aware of the experimental condition (i.e., synchronous versus asynchronous visuo-tactile stroking) and was replicated even when the stimuli eliciting the FBI[158] were presented unconsciously.

One of the most notorious recent conceptual developments is the specific interplay between prediction and PPS.[140,141,172] Indeed, a number of different groups utilizing vastly different techniques and populations have highlighted the strong role of PPS in inference. At the level of single units, for instance, Iriki and colleagues demonstrated that visuo-tactile neurons with depth restricted receptive fields fired not only when a visual stimulus was presented in close proximity, but also when the animals viewed a video in which a visual stimulus was presented close to their filmed body.[173] Furthermore, approaching visual stimuli activates neural areas consistent with PPS encoding, while equally enhancing tactile sensitivity selectively at the spatio-temporal predicted location of impact[140] (see Roncone *et al.*[174] for a similar predictive mechanism implemented in a robot's PPS). A similar role in detecting approaching exteroceptive stimuli or computing time-to-impact has been ascribed to PPS via an involuntary reflex mechanism.[175] Namely, Iannetti's group has shown that a blink reflex is induced via median nerve stimulation and these are most prominent in the near rather than far space. Interestingly, bringing one's arm toward the face results in a greater blink reflexes.[175] Equally highlighting the interplay between PPS and prediction/reliability—the latter a key concept within models of multisensory integration—Ferri and colleagues have shown that while mean BOLD responses to audio-tactile stimulation at different depths may not predict the size of PPS on an individual-by-individual basis, the intertrial variability of these responses in a typical PPS area such as the premotor cortex may accomplish this feat.[176] This finding implies a strong

predictive value to probability encoding in PPS representation. Lastly related to the role of PPS in prediction, a seminal observation by Fogassi and colleagues[138] suggested that the receptive field of PPS neurons expands when the velocity of incoming stimuli increases; as if to anticipate the moment of contact. Our group has recently demonstrated an analogous effect in humans, and by incorporating discharge adaptation in a neural network model of PPS[177,178] we were able to mechanistically account for the observation.[159] Namely, we have recently expanded on a neural network model of PPS[177,178] capable of replicating the plastic nature of PPS (e.g., the fact that it expands after tool use in the far space) to now equally replicate the dynamic nature of PPS (e.g., the fact that it reshapes as a function of the velocity of the incoming stimuli).[159] That is, while the model was previously capable of mimicking behavior that resulted from manipulations in the order minutes to hours, with the inclusion of a neural adaptation mechanism, it may now account for behavioral and neurophysiological findings that occur on a trial-per-trial basis (e.g., whether the particular stimulus is approaching quickly or slowly).

More directly related to bodily self-consciousness, a number of groups have shown that tactile stimulation of the body is not necessary to induce bodily illusions, but solely implying tactile sensation emanating from the PPS may elicit changes in bodily representation.[166,179–181] Furthermore, these tactile predictions may have a phenomenological correlate.[182] Guterstam and colleagues applied brushstrokes in mid-air at some distance above a rubber hand—without touching it—and in synchrony applied brushstrokes to the participant's hidden hand. Results suggested that this scenario resulted in body-like sensations between the brush and the rubber hand, and this sensation strongly correlated with the perception of the rubber hand as one's own. These authors, in turn, concluded that their illusion may be a perceptual correlate of visuo-tactile integration in PPS[166] (see Ref. 183 for a similar finding).

Taken together, thus, the PPS seemingly encodes for the perceived and not the true location of the body.[155,158] In addition, this space is highly malleable to multisensory experimental conditions, inclusively solely implied or inferred manipulations (e.g., suggested but not actual touch).[166,179–181] Hence, we argue that this space may be best understood as

a multisensory "stochastic bubble" coding for the probability with which a certain object will come in contact with the body (Fig. 2). This postulation does not obviate the precedent role ascribed to PPS in obstacle avoidance and body–environment interaction,[148] but simply reframes it. An interesting resultant question, thus, ought to be, To what extent is bodily self-consciousness stochastic? Indeed, as above-mentioned, general consensus is that at least partially we feel ownership over our bodies due to the spatio-temporal congruent multisensory information/evidence that is amassed over the course of our lifetime. Hence, as demonstrated by the broader study of multisensory integration, and as implied by the covered novel findings in PPS representation, bodily self-consciousness ought to be predictably altered given spatio-temporal configurations of stimuli and their respective reliabilities. In fact, novelty BCI models largely dependent on the relative spatio-temporal positioning and reliability of external stimuli (in addition to a prior for common cause) have started to be applied to the RHI and have shown that these models (as an example of a Bayesian model) may make interesting predictions[81] (similarly see Ref. 184 for a Bayesian account of out-of-body experiences resulting from misleading priors in the vestibular modality). Indeed, given BCI predictions, Samad and colleagues[81] suggested that the RHI may be induced without touch or even the appearance of touch (as undertaken in the above-reviewed studies) and their empirical findings corroborated the forecast. Samad[81] and colleagues' report thus supposes an important empirical contribution; yet, here we would like to emphasize their conceptual contribution by linking the RHI to a process of causal inference, and suggest that the PPS may be a spatial prior aiding in the causal inference computation scaffolding body ownership. Namely, as illustrated by Samad *et al.*[81] and others,[110] the RHI solely occurs within a limited region of space near the body, and this spatial extension is oddly similar to estimates of the peri-hand space.[156] Hence, putatively, the PPS acts as a spatial prior, where multisensory couplings involving the body are likely to occur on or near to the body (i.e., the PPS), but less likely to occur far from the body. Furthermore, taking the example of the remapping of PPS during the FBI;[155,158] in the case of congruent visuo-tactile stimulation in the far space, our brain's best prediction of the underlying causal structure of the
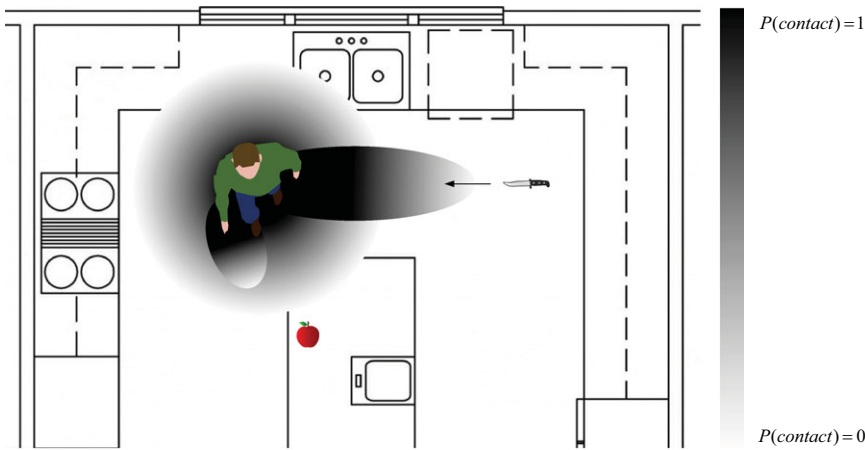
Figure 2. Peripersonal space (PPS) as a stochastic body space. We suggest that the PPS may be best understood as a stochastic space computing the likelihood that an object will come in contact with the body. That is, the likelihood that a somatosensory event will occur given the placement of exteroceptive stimuli in the environment. In the caricature, a number of different likelihood gradients exist; a general whole body one, predicting any kind of contact between the individual and the environment, one pertinent to the right hand, putatively approaching an apple, and finally one relating to the left space, that is, responding to the presence of an approaching treat.

world and body ought to be that we are located where we see our body being touched—aka, the likelihood of abundant synchronous visuo-tactile stimulation is incredibly small unless these refer to the same causal structure. In turn, the PPS remaps (e.g., the prior is updated) to engulf the space where we infer to be located. A similar rationale may be applied to out-of-body experiences,[131,134] in particular when incorporating vestibular anomalies.[184] This causal inference conceptual framework naturally engenders an array of interesting questions (i.e., what is the role of sensory noise/reliability in bodily self-consciousness? Is bodily self-consciousness impacted not solely by the integrative process of body-related sensory signals, but also the faithfulness with which external objects are represented?) and may permit borrowing a mechanistic explanation for bodily self-consciousness from the neurophysiological and computational characterization of visuo-vestibular integration by Angelaki and colleagues.[27,55,64]

The study of bodily self-consciousness is by default linked with the study of multisensory processes, and for the better part of two decades the field has been heavily influenced by the so-called principles of multisensory integration. However, as highlighted above, these principles are now taken to be but suggestions and solely apply to a restricted num-

ber of brain regions and tasks. In turn, it will be interesting in future work to leverage not only classical physiological findings in multisensory integration, but also modern computational principles (e.g., MLE, causal inference, and multisensory correlation detectors) and their mechanistic understanding (e.g., PPC and divisive normalization) in the study of bodily self-consciousness. We suggest that furthering existing models of PPS[177,178] to incorporate prediction and inference within their purview may be a particularly fruitful area of study. Namely, given the strong role of PPS in bodily self-consciousness, and the apparent affinity of this space to prediction, it may be possible to borrow modern multisensory computational frameworks and apply them within the framework of PPS in order to further our mechanistic account of bodily self-consciousness.

Leveraging the plastic body and translational opportunity

The preceding discussion has highlighted that the study of multisensory processes has morphed from specialized to subcortical areas to developing more general computational models applicable throughout the brain. Importantly, a mechanistic understanding regarding the neural implementation of Bayesian models is equally progressing. Bodily self-consciousness, in turn, has

departed from axiomatic principles and seems to be independently arriving at the conclusion that at least certain aspects of bodily self-consciousness (or its constraints, such as PPS) may be dictated by, or involved in inference computations. This theoretical standpoint implies that there is nothing special in the computation leading to bodily self-consciousness above and beyond an accrued history of congruent, body-related, and highly multisensory experiences. Indeed, the dependence on synchrony and spatial co-occurrence in many body-related experiments is in line with the principles of multisensory integration, which are in turn in line with divisive normalization[24,72] and a PPC[32,33] leading to statistical inference (see above). Similarly, the reliance on PPS is in many regards similar to the spatial rule of multisensory integration, which can be explained as above. The body-related visual information constraint is easily encapsulated by the notion of Bayesian priors, implying that nonbody parts in principle could be embodied—as suggested by a number of studies[179,185]—but this undertaking has to work against established priors (i.e., the fact that my hand looks like a stereotypical hand).

An outcome of these observations is that bodily representations are plastic and putatively involved in arenas seemingly quite distant from bodily encoding. Indeed, a number of recent studies have employed VR and different scenarios to experimentally manipulate bodily self-consciousness via multisensory stimulation and show the intriguing effects on higher order cognition. For instance, it has recently been demonstrated that by manipulating the perceived self-location of participants via the FBI, it is possible to alter the manner in which spatial and social concepts are perceived by showing that conceptual processing is referenced at the experienced location of the self, not the true location of the body.[155,158,186]

Other researchers have used multisensory paradigms yoked with realistic VR to induce ownership over avatars with differing gender,[187] age,[188] or race[189,190] vis-à-vis the participant. The appropriation over these different bodies leads to changes in implicit racial biases,[190] overt other-mimicry,[189] or object size-estimation,[188] to name a few. Causing an out-of-body experience during the course of a naturalistic conversation has been shown to trigger impairments in episodic memory for the particular social exchange,[191,192] impairments

that neuroimaging suggests are specifically associated with activity changes in the posterior hippocampus.[193] Putatively partially dependent on this memory impairment, embodying a virtual avatar and seeing this body mouth words while synchronous vibrotactile stimulation is given on participants' thyroid cartilage causes subjects to self-attribute the speaking to themselves and to shift the fundamental frequency of their later utterances toward the avatar's voice.[192] Interestingly, recently, misappropriations have equally been shown via a sensorimotor conflict. When participants perform a poking movement, and via a robotic device feel an asynchronous tactile rendering of their motor patterns on their own back (an impossible tactile feedback to their proprioceptive-motor signal), they report the presence of an invisible alien agent—the culprit of the motor command participants feel on their back.[129] Interestingly, similar reports of alien voices and delusions of control are well documented in schizophrenic populations,[194] and hence the mentioned results reinforce the previously proposed notion that positive symptoms in this psychopathology may emanate from impairments in sensorimotor and multisensory integration.[195] Clinicians and researchers documenting the multisensory perceptual abilities of individuals with psychopathological conditions have equally reached this conclusion.[196–199]

Evidently, the study of the impact of bodily self-consciousness on higher order cognition and its role in psychopathology (see above) is in its infancy (particularly regarding mechanisms). However, conceiving of the PPS and bodily self-consciousness generally as outcomes of a statistical inference problem, and subject to priors, allows for the putative impact of these computations in cognition. Namely, this conception reinforces the fact that perception—inclusively that of one's own body—is dictated by priors and sensory likelihoods. In turn, the priors reflect accumulated history of sensory likelihoods, and hence if low-level sensory processing is altered, over the course of many exposures, priors—cognition—will be distorted as well. Fittingly, multisensory integration is well documented to be anomalous in autism spectrum disorder[197,199–203] and schizophrenia (SZ),[84,196,204] among other psychopathologies,[205] and these—in particular SZ—are considered to be disorders of the self.[186,206] Furthermore, much of the recent

evidence suggesting deficitary sensory processing in psychopathology is highlighting the presence of either weak or inflexible priors.[207–211] Anomalously small PPS representations have also been indexed in SZ,[212] suggesting that perhaps these patients do not make use of their stochastic body space. In other words, the anomalous spatial prior that SZ possess in coupling bodily and nonbodily-related stimuli (i.e., their ill-defined PPS) may underpin their reported overextended sense of presence and loss of self-other boundary.[105,213] See Noel *et al.*[186] for further discussion of the role of bodily self-consciousness and PPS in psychopathology.

Overall, given the widespread availability of VR technologies and soaring neuroscientific evidence indicating how to design appropriate multisensory and sensorimotor environments (including the human body), we are already seeing a number of clinical trials using these approaches for the treatment of neurological conditions.[214,215] As alluded to above, the next frontier is likely the psychiatric domain.[216]

Conclusions

Two decades ago, the relevance of studying not individual sensory modalities in isolation, but as a collective, was brought to the forefront. Evidently, in addition to offering the opportunity to study the process of neural integration—arguably a foundational block for all neural undertakings—this focus implicitly launched neuroscientific inquiry from the laboratory to the natural world. The early studies delineated the basic principles governing multisensory integration in a relatively simple subcortical area, and have in the last 10 years morphed into general computational principles involving statistical inference. Moreover, in the last 5–10 years, the neural underpinnings of multisensory statistical inference have been greatly elucidated. The study of bodily self-consciousness, a field complementary to and rooted in the study of multisensory integration, has on its side in the last decade outlined the basic necessities and constraints involved in full-fledged embodiment. From an empirical standpoint, this field has made great progress in outlining the brain areas involved in bodily self-consciousness, and in associating this process with the multisensory integration of bodily signals within the PPS. In addition, more recent work has shown how PPS, and consequently bodily self-consciousness to some extent, is

plastic and further impacts other areas of perception and cognition. We argue it is now time to delineate not only conceptual or neurocognitive models but also computational and eventually neural network models of bodily self-consciousness. This area is ripe for progress considering that conveniently many of the principles involved in multisensory integration equally apply to PPS representation, and thus seemingly the recent computational principles uncovered in this latter field may equally be borrowed. Finally, the field of bodily self-consciousness has embraced emerging technologies, such as VR, and exemplified how these technological developments coupled with scientific understanding may impact society as whole (e.g., using VR, racial bias is starting to be explained not by ill-defined mental processes but by low level multisensory processes[189,190]). Indeed, although there is undoubtedly still a host of open questions both within the study of multisensory and bodily neural encoding, researchers, clinicians, and inclusively entrepreneurs have commenced to leverage this scientific understanding in areas far from basic neuroscience research.

Acknowledgments

Competing interests

The authors declare no competing interests.

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