The Contributions of the Bodily Senses to Body Representations in the Brain

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Forthcoming in Review of Philosophy and Psychology

Felix reaches up to catch a high line drive to left field and fires the ball off to Benji at home plate, who then tags the runner trying to score. For Felix to catch the ball and transfer it from his glove to his throwing hand, he needs to have a sense of where his hands are relative to one another and the rest of his body. This sort of information is subconsciously tracked in the body schema (or postural schema), a representation of the current bodily posture that is updated on the basis of proprioceptive inputs (Head 1920; Pallaird 1999; Gallagher 1998). While the existence of the body schema in not in dispute, its origin is. After reviewing the competing proposals (§1), I introduce the conceptual tools needed to move the debate forward (§2) and apply them to the question of the extent to which the body schema could be learned from perceptual input *in utero* (§3-§4). I argue that it could give rise to something recognizable as the body schema, though not quite rising to the level of the mature body schema. After considering the implications for further research on the origins of the body schema, I show how these results apply to other body representations, helping clarify the vexing question of the number, nature, and interactions among body representations in the brain. This theoretical work also promises to advance our understanding and treatment protocols for disorders affecting such body representations (e.g., anorexia nervosa) (§5).

1. The Origins of the Body Schema

The traditional view is that the body schema is acquired after birth via coordination of sensory inputs from different modalities (primarily touch, proprioception, and vision) and, perhaps efference copy (Piaget 1962; Wittling 1968; Assaiante et al., 2014) – e.g., an infant learns that certain proprioceptive inputs correlate with certain visual stimulation when she moves her right arm in front of her face. Such correlations are thought to be learned through more or less random self-motion in early childhood. More recently, it has been proposed that the body schema is already present at birth.

On one version of this proposal the body schema is an innate endowment genetically hardwired into the fetus (Gallagher et al., 1998 Gallagher 2005; Rochat 2001; Bhatt et al., 2016).[1] On the second present-at-birth approach, the body schema is acquired by a process of exploratory self-motion – as with the traditional view – but this process, called body babbling or motor babbling by its proponents, begins *in utero* (Meltzoff and Moore 1997; Meltzoff 2007a, 2007b; Marshall and Meltzoff 2014, 2015; Meltzoff and Marshall 2018; Fagard et al. 2018).[2] In the course of the exploratory self-motion, tactile sensation provides sensory feedback as body parts come into contact with one another or with the uterine wall. This is combined with proprioceptive input to determine the relative positions of body parts and how they correlate with various movements available to the fetus.

Both present-at-birth views are inspired by results suggesting that extremely young neonates can imitate facial expressions and hand gestures (Maratos 1982; Meltzoff and Moore 1977, 1983, 1989, 1992, 1994; Kugiumutzakis 1999; Nagy et al., 2005; Nagy et al., 2014; Ullstadius 1998; Simpson et al. 2014). The idea is that an infant would need a body schema to represent the position of, say, their tongue to imitate an experimenter sticking their tongue out at the infant. Assuming that the support for neonatal imitation is adequate, the inference to a body schema at birth is supported. However, imitation studies cannot tell us whether the body schema originates with body babbling or with innate endowments. To decide between these alternatives, we need to know if there is sufficient sensory input to generate the

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[1] Gallagher and colleagues acknowledge that there is no evidence for representations of congenitally absent limbs in the body schema (e.g., we don't see behaviors that indicate that action planning proceeded as though the missing limb were present), which their view would predict. To circumvent this difficulty they propose that, in the absence of sensory stimulation *in utero*, innate representations of the affected body parts in the body schema will atrophy, dwindle, and perhaps even disappear (Gallagher et al. 1998; Gallagher 2005).

[2] In its initial presentation, body babbling was invoked as part of an explanation of infant imitation of facial expressions that was inspired by verbal babbling accounts of the learned mappings of articulatory gestures and the resulting vocal sounds (Meltzoff and Moore 1997). The idea has since been expanded in work by Meltzoff and Moore to explain whole body imitation (1989, 1992, 1994). The resulting account of infant imitation then relies on intermodal equivalences established between the body schema resulting from body babbling and visual representations of others' bodies (Meltzoff and Moore 1997, pp. 7-8). The origins of this cross-modal equivalence are left unexamined.

body schema *in utero*. If there is, this places pressure on the innate view: The innate endowment view requires body babbling-like movements to *reinforce* the innate schema (see n.1). If such movements are also sufficient for *forming* the schema, then there is an argument from parsimony in favor of the body babbling hypothesis.[3] If there is *not* sufficient sensory input for the formation of a body schema, this lends support to at least some innate endowments. The key question, then, is whether sensory information available *in utero* is sufficient for the formation of an imitation-supporting body schema without the support of innate endowments of the sort proposed by Gallagher and colleagues.

However, these infant imitation studies are highly controversial (Jones 2009; Ray and Heyes 2011; Oostenbroek et al., 2016; Oostenbroek et al., 2018). So we cannot yet rule out the traditional view. Of course, failure to show imitation doesn't guarantee that there is no body schema present at birth. There are other factors that are necessary for imitation that could be lacking, thereby explaining the failure to replicate the imitation results – e.g., social motivation (Bremner 2017, p. 6). So all three of our alternatives (the traditional view, body babbling, and innate endowments) are still on the table.

If the controversy around neonatal imitation is resolved in favor of non-imitation, then the proponent of a present-at-birth body schema must fall back on other studies of *in utero* movements and corresponding brain activity. To date these studies have focused on brain activity in preterm neonates to neonates no more than 60 days old (who are thought to be roughly on par with near term fetuses in terms of brain development). These studies provide support for the existence of body maps in the neonatal/fetal brain (Müller 2003; Milh et al., 2007; Marshall and Meltzoff 2014, 2015; Nevalainen et al., 2015; Meltzoff and Marshall 2018; Fagard et al. 2018; Meltzoff, Saby, and Marshall 2019). Several authors claim that these results provide evidence of a functional body schema in the fetus (Marshall and Meltzoff 2014, 2015; Fagard et al., 2018; Meltzoff, Saby, and Marshall 2019).[4]

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[3] The argument is further strengthened by the consideration that the fetus's body undergoes substantial developmental changes in size and relative proportions of body parts, which would mean that any innate schema would need to be continually updated through the process of development.

[4] These accounts also reference observations of seemingly goal-oriented movements of the fetus *in utero* (e.g., opening the mouth in apparent anticipation of the arrival of the hand; Myowa-Yamakoshi and Takeshita 2006; Zoia

However, these studies do not rule out (i) a role for fetal movements that is restricted to contributing to the organization of neural pathways resulting in the somatotopic organization of the primary somatosensory cortex and motor cortex corresponding to the homunculi (fig. 1) of the somatosensory and motor cortices and (ii) a role for genetically programmed developments of the body schema that prefigure (or are accompanied by) fetal movements of the corresponding body parts.

The idea behind (i), which can be taken as a traditionalist response to the body babbling interpretation of these results, is that fetal movements merely help organize somatosensory cortex (S1) into a somatopic map known as the sensorimotor homunculus (Penfield and Boldrey 1937; Penfield and Rasmussen 1950). The homunculus is the primary destination of pre-cortical tactile and proprioceptive pathways and has traditionally been viewed as a sensory relay, not as functional representations of the spatial organization of the body.[5] In particular, it is not thought to function as the body schema. Two features of the homunculi support this view (1) the homunculus is distorted in a way that would undercut the accuracy of the representation of limb positions in the postural schema and (2) the structural organization of the homunculus does not correspond to that of the body, itself.[6] And even if (1) and (2) were not true, a structural correspondence between neural structures and the body is neither necessary nor sufficient for those neural structures to implement a representation of the body's structure. Therefore, if the brain activity and movement patterns seen in very young neonates is merely indicative of the organization of the homunculi, it does not support the presence of a body schema at birth.

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et al. 2007; Reissland et al., 2014) to bolster this interpretation. The extent to which these seemingly anticipatory behaviors are *in fact* anticipations of the outcomes of planned actions is open to debate.

[5] There are multiple hierarchically arranged homunculi found in Brodmann areas 3a and 3b of S1. Those of 3a are primarily associated with proprioception, those of 3b primarily with touch. While these take their primary input from their associated peripheral receptors (proprioceptors and mechanoreceptors in the skin, respectively), they also take inputs from elsewhere. For instance, there are projections to S1 from non-somatosensory nuclei of the thalamus– particularly nuclei that take multisensory inputs. The function of these projections is currently unknown, as is whether they remain wholly somatosensory, but are routed through nuclei that also receive inputs from other senses, or include inputs from other senses. Similarly, inputs to S1 related to proprioception (Brodmann area 3a) are largely restricted to input from the various peripheral proprioceptors. Unsurprisingly, 3a has extensive, reciprocal connections with motor areas.

[6] A recent study suggests that the somatosensory homunculus might play a role in the representation of body metrics and, so, is more than a sensory relay (Giurgola et al., 2019). Nevertheless, the body schema certainly involves more than just the homunculi.

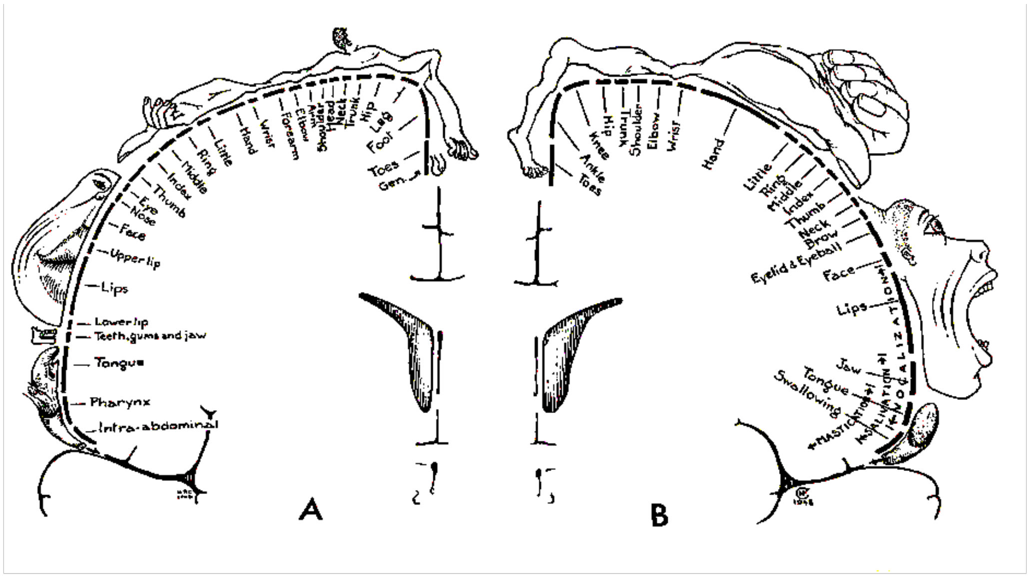

Fig. 1 *1954 Penfield Homunculi*: **(A)** Sensory homunculus. **(B)** Motor homunculus. (Image from the Penfield Archives, Osler Library of the History of Medicine.)

Nevertheless, the neurological evidence indicates that fetuses have sensory experience and engage in movements similar to those that the traditionalists cite as sources of knowledge about the body acquired postnatally. It would be surprising if *no* learning relevant to the formation of the body schema were accomplished *in utero*, even if that learning falls short of a functional body schema (de Klerk et al., 2021). The key question, here, is *how much* perceptual learning, relevant to the body schema, is accomplished *in utero*.[7]

To address (ii), we should consider what predictions the innate endowment view makes that will distinguish it from the body babbling hypothesis. This is particularly challenging given the reinforcement role posited for fetal movement by nativists. To escape the parsimony argument, the proponent of innate endowments will need to show that these endowments are necessary for the formation of the body schema

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[7] Of course, the body schema might not begin to develop until infancy due to the absence of relevant sensory input or insufficient brain maturation. To fully address (i), we would need to find activation in brain areas associated with the body schema (e.g., the posterior parietal cortex) beyond the homunculus. One difficulty is that current research on neonatal brain activation during somatosensory stimulation is that it uses EEG, which has relatively poor spatial resolution. More finely resolved technologies (e.g., fMRI) are difficult to use with infants. We could also address (i) by examining behavioral evidence for or against action planning or awareness of limb positions in fetuses and very young neonates as well as evidence for or against repetitive movements that could generate sensory information about the size and position of limbs *in utero*. These behavioral observations will, however, bring interpretive difficulties.

– sensory input alone will not suffice. So once again, we need to consider whether there is sufficient sensory input *in utero* to generate a body schema.[8]

In sum, the question we need to answer to adjudicate between the three competing accounts of the origin of the body schema is: How much is acquired *in utero* and does it amount to something properly called a body schema? My goal, in the next three sections, is to move us closer to an answer to this question by determining if a body schema *could be* derived from body babbling *in utero*.

2. Information and the Minimal Bodily Senses

To begin, we need a way to assess the potential sensory contributions to the formation of a body schema *in utero*. The sensory contributions come from the bodily senses – touch, proprioception, and equilibrioception. (Visual input – the other primary sensory contributor to body representations – is too impoverished *in utero* to be much help (but see §5.1).) I understand these sensory contributions in terms of body-relevant information supplied to the body schema. It will be helpful, then, to specify what counts as a relevant bodily sense in this context, what is meant by information, and how that relates to representation (which is, after all, what the body schema is).

The relevant notions of these bodily senses are not the mature proprioception, touch, and equilibrioception of adult experience. They are, rather, the earliest developmental stages of what will later become these mature senses.[9] The evidence that fetal movements play a role in the somatotopic

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[8] If neonatal imitation is not supported, the innate endowment theorist will need to point to some achievement that implicates the body schema prior to the child having sufficient sensory experience to acquire the body schema.

[9] This is one key sense in which the present project differs from a recent paper by Skrzypulec (2023), who focuses on the contributions of mature bodily senses to body representations (though he omits equilibrioception). Also, while I focus on the body schema, Skrzypulec is primarily concerned with bodily awareness and, hence, the body image (see section 5.2). In particular, Skryzpulec is concerned with the bodily senses' contributions to mereological as well as topological aspects of bodily awareness. I am only concerned with topological aspects of the body schema. Our methodologies differ as well. Skryzpulec relies on empirical results from behavioral studies to support his conclusions. I begin from a place of greater skepticism about these studies and argue from basic facts about the structure of the peripheral sense organs of the bodily senses and principles concerning the conditions under which the stimulation of these senses can capture information that could contribute to the formation of a body schema. As such my account focuses on what is *possible* but not necessarily actual as a guide for future empirical work (see n.15). Skrzypulec takes aim at what the *actual* contributions of the bodily senses to the structural content of bodily awareness.

organization of S1 and the fact that there are distinct regions of the primary somatosensory cortex (S1) for processing proprioceptive and tactile inputs (Brodmann areas 3a and 3b, respectively) suggests that these input streams are first organized separately and are integrated at a later stage of development. Therefore, it will be advisable to take extremely minimal notions of the senses – first in isolation, then in combination – as our starting point.[10] As a first pass, we can say that the minimal bodily senses receive input from the stimulation of their peripheral receptor organs – e.g., pressure on the skin for minimal touch, stretching of muscle fibers and tendons for minimal proprioception, mechanical stimulation due to acceleration of hair cells in the vestibular labyrinths for minimal equilibrioception – and engage in only shallow processing thereof, prior to any interactions with other sensory inputs.

Regarding the information carried by the minimal bodily senses: A perceptual mechanism, M, carries information about a condition, C, obtaining just in case (a change in) the state, S, of M makes it more or less likely that that state of affairs obtains (i.e., $\Pr(C) \neq \Pr(C|S)$). To carry information about a state of affairs is not necessarily to represent that state of affairs, but our ultimate goal is a representation of the body's current posture (the body schema). On the framework I am adopting – an informational teleosemantic account of representation (Neander 2017; Shea 2018) – the representational content attributable to some state of a perceptual mechanism is derived from a subset of the information carried by that mechanism. It is that subset of information that is *used* by cognitive processing to perform some aspect of its function.[11]

Therefore, I will concentrate only on the information available for use – what I'll call encoded information – and will focus on the ability of the minimal bodily senses to encode information concerning

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[10] These facts, along with the fact that the relevant self-motions are thought to be random at first, motivates my focus on sensory contributions to the body schema. Any contribution from motor planning will be subsequent to the formation of a rudimentary body schema from perceptual resources, on this picture.

[11] Accounts differ on their characterization of the relevant information and functions, but this generalized picture will do for present purposes. Also note, perceptual representations are representations that some state of the world obtains. The probabilistic component is not generally thought to be part of the representational content, though it may continue to have an impact on metacognition about one's perceptual states (e.g., how confident one is that the world is as perception represents it to be).

the position of body parts relative to one another.[12] Given what I have said about the relationship between encoded information and representation, this is a necessary precondition of the formation of a *representation* of the current body posture (the body schema). Since the role of the body schema is to make the current bodily posture available to motor processing, encoded information about bodily position will be represented in the body schema because it will be *used* by, e.g., motor planning. If the relevant information could be encoded by the minimal bodily senses, it could underwrite a dynamic body representation corresponding to the body schema. A (change in) total state of a perceptual mechanism will encode information in the following condition.[13]

> **Perceptual Encoding.** Information, I, regarding a condition, C, obtaining will be encoded by (a change in) the total state, S, of a perceptual mechanism, M, iff
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> (i) the activation state of the peripheral sensory receptors, along with the implementation of any algorithms applied to those stimulation states by M (or mechanisms preceding M in the perceptual processing stream), causes M to be in S, and
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> (ii) the activation state of the peripheral sensory receptors, the implementation of any algorithms applied to those stimulation states by M (or mechanisms preceding M in the processing stream responsible for M's being in S), and any background information carried by M (or mechanisms preceding M in the processing stream responsible for M's being in S) collectively determine I.[14]

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[12] Phrased this way, the problem looks very much like the forward kinematics problem – the problem of determining a particular effort's location in external space, given information about joint angles. Indeed, solving the forward kinematics problem is a primary function of the body schema. However, solutions to the forward kinematics problem assume things that we cannot when assessing the body babbling hypothesis – e.g., the lengths of limb segments (see §3).

[13] Some authors have referred to information made available to further processing as *explicit* information and information that is not passed along to further processing *implicit* information (e.g., Shea, 2015, p. 79). Implicit/explicit information, on these characterizations is mechanism-relative – information that is available internally to the mechanism might not be made available by its output – and comes apart from implicit/explicit representational contents. To prevent confusion, I will avoid using 'implicit' and 'explicit' with respect to information, focusing instead on whether the relevant information is encoded.

[14] The relevant sense of determination is determination by the laws of nature or law-like regularities. The idea is that we only consider correlational information that results when we restrict the basis for calculating Pr(C|S) to the overall state of the perceptual mechanisms and activation states of receptors, the laws of nature, and background

The reason for the determination requirement is to ensure that all the background information contributing to the perceptual processing is accounted for as such – as opposed to smuggling it into information attributed to the sensory stimulation by appeal to something like Dretske's channel conditions (1981, p. 115-116). These correlations *will* be accounted for in the analysis, but in a way that makes the question of whether the information is learned or innate tractable: Once we have disentangled the contributions of occurrent sensory stimulation from those of background information, we can further assess whether the background information could be acquired from perceptual learning (by observing regularities in past sensory stimulations) or if it must be innate (see below).

The goal here is to identify the *maximum possible* contributions of sensory stimulation using the *minimum necessary* innate endowments required to arrive at the body schema *in utero*.[15] The relevant *in utero* sensory stimulation will be that received by the minimal bodily senses. Other sensory inputs – especially visual input – that are relevant to the formation of a body schema are available in only highly attenuated form until outside the womb. I will now say a bit more about the roles of occurrent sensory stimulation and background information in perceptually encoding information.

Occurrent sensory stimulation. Recall that the minimal bodily senses are distinguished by the shallow processing (prior to interaction with the other senses) of stimulation of their peripheral sensory receptors. The peripheral receptors of each minimal bodily sense include: (1) a set of transducers that

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information carried by the mechanism. The information that is encoded is information concerning C where $\Pr(C|S) \neq \Pr(C)$, when $\Pr(C|S)$ is calculated with these restrictions in place. This rules out the encoding of, e.g., merely locally reliable (and, hence, not law-like) correlations without background information concerning those correlations. It is beyond the scope of this paper to spell out exactly how strict the regularity must be to count as 'law-like'. It will, however, need to be quite strict to serve the purpose described below. (Note, too, that in perceptual encoding we are generally interested in the case where C obtaining is made more, not less likely, given S – i.e., cases where $\Pr(C|S) > \Pr(C)$.)

[15] What I am advocating is akin to a 'how-possibly explanation': an explanation of how a phenomenon could be generated or sustained by a mechanism. How-possibly explanations are contrasted with how-actually and how-plausibly explanations; see Carver and Darden (2013, pp. 34-35). Typically, a how-possibly explanation decomposes the mechanism into its components and these components are given a functional analysis that explains the operation of the higher-level mechanism they compose (Bechtel 2008; Bechtel and Abrahamsen 2005; Craver 2002, 2003, 2005, 2009; Darden 2002; Craver and Darden 2001, 2005, 2013). I am recommending that we look to the functional contributions of proposed inputs to the body schema-generating mechanism as a means of getting a better understanding of the operation of that (high-level) mechanism – a mechanism we have yet to locate in the brain.

respond to some feature or other of the sense's characteristic proximal stimulus, and (2) a receptor organ – a continuous surface throughout which the transducers are distributed.[16] We can get a rough-and-ready individuation of the minimal bodily senses in terms of receptor organ types: minimal touch's receptor organ is the skin; minimal proprioception's, the connective tissues of the musculoskeletal system; minimal equilibrioception's, the vestibular labyrinths.[17] In the case of minimal equilibrioception, there are multiple receptor organs of the same type – the left and right vestibular labyrinths – whose inputs must be coordinated. The transducers of the bodily senses are the specialized mechanoreceptors found in their respective receptor organs. These mechanoreceptors transduce mechanical energy into neural signals.

The (change in) activation of an individual transducer (e.g., a mechanoreceptor in the skin) will encode the degree of (change in) stimulation by its characteristic stimulus (e.g., pressure): The degree of stimulation is both the condition (C) about which information is being encoded and the source of the occurrent stimulation to the transducer (M). The transducer responds to this stimulation in a law-governed way by converting the mechanical stimulation into neural impulses (going into S). Given this, $Pr(C|S) > Pr(C)$, so M's going into S carries information (I) about C. And, given that M's performing A is a law-governed response to the stimulus, the occurrent stimulation of the transducer nomically determines – and hence encodes – I. (No background information or algorithms are brought to bear at this stage.)

Of course, very little is gained by looking at the activation profiles of single transducers – a single receptor in the skin, for instance, will only respond to very localized stimulation. It is only when (changes to) the activation states of receptors working in concert are considered that we begin to see reliable and informative input concerning the stimulation of the bodily surface. So we will need to posit algorithms for tracking the activation states of multiple receptors on the particular organ throughout which they are

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[16] For a well-known example outside of the bodily senses, think of rods and cones (transducers) on the retina (receptor).

[17] Transducer type factors in distinguishing the minimal senses from one another when transducers on a single receptor organ respond to different sorts of stimuli. For example, the skin contains distinct transducer types for pressure, pain, and heat. We want to be able to consider each of these individually before considering their interactions. Here we will just be concerned with tactile pressure sense (the receptors of which are the most spatially sensitive of the three).

distributed. This is why the physical continuity of the receptor organ is important. It guarantees that its transducers will behave in a law-governed way (given the physical interaction of the receptor with the stimulus and the distribution of transducers on the receptor) that can be exploited by these algorithms.[18] Clearly, then, algorithms will depend on *some* background information.

Background information. The algorithms operating on the sensory inputs to the minimal bodily senses utilize background information that allows sensory processing to transform the information made immediately available by occurrent sensory stimulation into more useful information. For instance, background information about the distribution of transducers in the skin is necessary to extract the shape of a stimulus pressing on the skin from the occurrent sensory stimulation of pressure-sensitive mechanoreceptors. These algorithms can also apply to distinct receptor organs of a single minimal sense (e.g., the vestibular labyrinths) and – to effect the integration of the bodily senses – to receptor organs of distinct minimal bodily senses.

Some of this background information could be learned – e.g., information concerning invariant features of the perceptual apparatus can be acquired given the law-like regularities they impose on stimulation states. Other background information might be innate. To illustrate with an example from audition: A mechanism translating time differences in the arrival of a sound wave at the left and right ears into directional information will require information concerning the interaural distance and the unity of the stimulus. The mechanisms translating interaural time differences into directional information are conditioned by visual inputs (Bajo et al. 2010; Bajo and King 2013; Brainard and Knudsen 1993; Budinger et al. 2006; Feldman and Knudsen 1997; Peterson and Schofield 2007). The implication is that learned correlations between visual, auditory, and proprioceptive stimulation are used to derive the

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[18] Contrast with distinct (non-continuous) receptors of a given type: Vision (with its retinas) and audition (with its cochlea) are both subject to illusions arising from distinct stimuli being presented to each of the modality's receptor organs (e.g., by stereograms or stereo headphones).

interaural distance, a (relatively) invariant feature of the perceiver's perceptual apparatus.[19] The assumption of the unity of the stimulus is more likely to be innate.[20]

Turning back to the body schema: The body schema will need background information about the spatial relationships between mechanoreceptors of minimal touch and minimal proprioception, and the size and shape of the intervening limb segments, to transform information encoded by the occurrent sensory stimulation of proprioceptors into encoded information about the body's current position. This background information might be acquired (e.g., via body babbling *in utero*) or it might be the result of an innate endowment.

Given our task of assessing the maximum possible contributions of perceptual learning to the formation of the body schema, we are only warranted in attributing innate information about such correlations once we have exhausted the possible contributions of occurrent stimulation and acquired background information, but we still find that the correlations are needed. And so, before attributing innate information, we must first consider whether there is a sufficient degree of uniformity in correlations obtaining among some subset of past stimulations to support learning of, e.g., spatial relations between sensitive portions of the skin from the regularities in adjacent stimulations. If there is not, but the most perspicuous functional analysis of the perceptual mechanism requires this information, then we are warranted in attributing it as innate information.

In this way, we can account for the correlations that have been ruled out by the determination condition by including information about these correlations in the background information captured by the analysis. And it allows us to do so in a way that minimizes innate attributions while maximizing the contributions of sensory input, which is exactly what we need to assess the maximum possible contributions of sensory stimulation to the acquisition of a body schema *in utero*.

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[19] Insofar this information is derived from learned correlations between visual, auditory, and proprioceptive input, and this input includes a mapping of points in visual space to interaural time differences, there will be no need to *represent* the interaural distance (i.e., use it in the course of perceptual processing).

[20] The account of encoding for innate contents remains an open question. For present purposes I will answer it obliquely (see below).

3. Minimal Proprioception and Minimal Touch

We are now in a position to assess the possible contributions of the minimal bodily senses to the formation of the body schema. I begin with minimal touch and minimal proprioception, as these provide much more of the relevant information concerning body structure needed for the body schema than does minimal equilibrioception.

3.1. Minimal Touch

The mechanoreceptors of minimal touch are found in the skin and are responsive to pressure, torsion, and tension.[21] While our ordinary sense of touch gives us the perception of shape, size, and surface texture of the objects manipulated, this requires information regarding the size and shape of the body part receiving the tactile stimulation as well as information about the spatial distribution of the stimulation of mechanoreceptors made by the pressure exerted by these objects on the skin's surface. Moreover, it requires information about the current position of the body parts receiving the stimulation: stimulation of the palm and underside of the fingers indicates one shape when the hand is held flat and another when it is cupped. That is, ordinary touch requires the body schema.[22] The question before us is how tactile

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[21] Different receptor types respond to different sorts of stimulation on a different timescale (slow and fast adapting). Fast adapting: Meissner's corpuscles detect continuous movement along the skin's surface via low-frequency vibration. Pacianian corpuscles respond to pressure and vibration. Slow adapting: Merkel's disks respond to light pressure. Ruffini endings respond to stretch. Ruffini endings also provide input to proprioception. We will largely pass over them in minimal touch, returning to them when we consider the combination of minimal touch and minimal proprioception.

[22] The claim here is that this information is necessarily a part of the subpersonal processing underwriting tactile experience. It is not that ordinary tactile experience, itself, is mediated by conscious representations of, e.g., the shape of surfaces pressing on the skin. Matthen (2021) makes this point in his discussion of tactile vs. haptic sensation, where tactile sensation is merely informed by the mechanoreceptors of the skin while haptic sensation can include inputs from other sources (in particular, proprioception and vision). Matthen argues that tactile sensation is very weakly spatial, if spatial at all, for reasons roughly akin to those I offer below with respect to minimal touch. A few key differences between my treatment and Matthen's: Matthen is concerned with sensation – and, hence, with *perception* – whereas I am concerned with (subpersonal) informational contributes to the formation of the body schema, which informs *action*. Also, while we both offer arguments citing the receptive fields of mechanoreceptors in the skin, Matthen's treatment does not include a discussion of possible contributions of the skin's stretch receptors. As a result, his conclusion regarding the spatiality of tactile sensation is more pessimistic than mine concerning the spatial properties of the body encoded by minimal touch.

stimulation, *prior* to the development of the body schema, can contribute to the formation of that representation. In particular, the question is what minimal touch – the sense of touch we can expect fetuses to have – can contribute to the body schema. Of particular interest will be the ability of minimal touch to contribute to the acquisition of information about the size and shape of the body, which must combine with information about joint angles to determine the present bodily position (the very thing the body schema is supposed to represent).

Imagine a pencil laid lengthwise along your forearm. The pencil stimulates a number of pressure sensors embedded in the skin. Minimal touch encodes the degree of stimulation at mechanoreceptors *a*, *b*, and *c*, along the length of the pencil, but not the relative lengths of *ab* or *bc* or whether these lie along a single straight line, turn a corner at some angle, or lie along an arc. Indeed – for all we've said – minimal touch won't even tell us that the stimulus is continuous between *a*, *b*, and *c*. That is, it won't differentiate stimulation by the pencil or by a comb whose teeth are spaced so as to fall right at the mechanoreceptors (holding pressure of the stimulations constant). Our algorithms will be no help here: No set of *discrete* transducer states (of minimal touch) can distinguish the two stimulations. And so occurrent stimulation of minimal touch won't encode the continuity of the stimulus/stimulated region of skin along *abc*, given the determination criterion for encoding.

However, there is more to say: These mechanoreceptors have overlapping receptive fields (RFs). Each RF is an area of the skin, stimulation of which will activate its associated mechanoreceptor. The mechanoreceptor will be most sensitive at the portion of the RF closest to it, but will respond to the immediately surrounding areas as well (fig. 2). Given the overlap of the RFs, differences in activation of a mechanoreceptor, due to location of the stimulus relative to its RF, can underwrite the learning of continuities between RFs. Trace a finger along your forearm. At any given time, your fingertip will stimulate multiple overlapping RFs. As you move your finger, it will leave the RFs of some mechanoreceptors, remain in the RFs of others, and enter the RFs of previously unstimulated mechanoreceptors. Learning the regularities in coordinated RF responses (self-initiated or otherwise) will establish the continuity of the RFs as background information that can be used in conjunction with algorithms that take input from multiple mechanoreceptors (with a continuous RF structure) and he occurrent stimulation of those mechanoreceptors.[23] With these resources we can differentiate stimulation by the pencil (continuous region of the skin) and the comb (discrete points).[24]

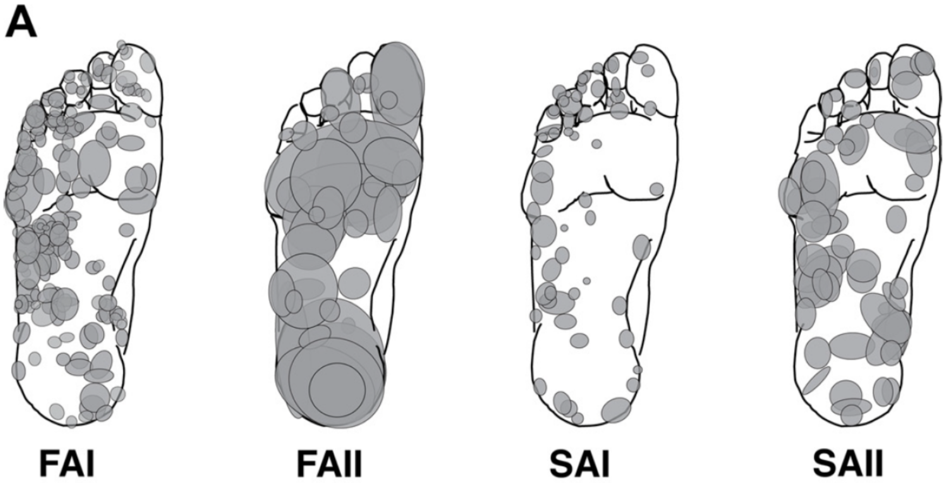

Fig. 2 RF architecture of foot by mechanoreceptor type, from Strzalkoski et al (2018, p. 1236). 'FA 'stands for 'fast adapting. 'SA 'stands for slow-adapting. 'I 'indicates small RFs, 'II 'large RFs. FAI mechanoreceptors are also known as Meissner's corpuscles, FAII as Pacianian corpuscles, SAI as Merkel's disks, and SAII as Ruffini endings. See n.21 for a description of each mechnoreceptor type's function.

By extension, we can acquire background information about the continuity of the skin's surface from sensory input. (There are no areas of the skin not in the RF of some mechanoreceptor.) However, this falls far short of information about the size and shape of the body/body parts. Consider a creature, Feelix, whose only sense is minimal touch.[25] Feelix will be able to learn that he has a continuous surface, and, to some extent, Feelix can use this information to localize stimulation on his skin. He will be able to encode the location of the stimulation relative to individual mechanoreceptors when, e.g., a pencil is laid

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[23] We can also appeal to hierarchies of RFs, with a later stage of processing having a RF that incorporates those of multiple mechanoreceptors. Such downstream mechanisms will implement the sorts of algorithms we rely on for encoding based on the stimulation states of multiple transducers. There is evidence for such hierarchical processing of tactile stimulation with the RFs expanding as we ascend the hierarchy and, at higher hierarchical levels, these larger RFs are tuned to particular spatial patterns of stimulation analogous to those in the hierarchical processing of visual forms.

[24] Which is not to say that there are no limits to our ability to distinguish continuous from multiple discrete simultaneous stimulations or that there could not be illusions of continuity introduced by some abnormal stimulus.

[25] Praise or blame for the name goes to [OMITTED FOR ANONYMOUS REVIEW].

somewhere upon the surface of his skin. He will encode that a continuous region of skin is stimulated, given the overlapping RFs. But no amount of stimulation of minimal touch, alone, will allow Feelix to acquire information about the spatial disposition of each mechanoreceptor to the next or the size and shape of the RFs: To get distance of a stimulation in an RF from the location of the mechanoreceptor of that RF – which is a precursor to getting the size and shape of an RF and the spatial disposisiton of individual mechanoreceptors – we would need a lawlike regularity between intensity of the stimulation and distance from the mechanoreceptor. But a light touch near the mechanoreceptor can yield an equivalent response to a stronger touch further from the mechanoreceptor. So for all Feelix knows, the continuous region of stimulation might be long or short, wider or narrow, curved, straight, angled, etc.[26] Hence the size and shape of stimulated regions of the skin is not determined by the occurrent stimulation and background information acquired from past stimulations of minimal touch. Therefore, it won't be encoded.

Given the foregoing, Feelix won't encode the size and shape of his body parts or their present positions relative to one another, as is necessary for a body schema: Imagine Feelix as a bit of silly putty. Draw a boundary around some region of Feelix's surface. Feelix would be able to register that a stimulation falls within this region, but he will not register the region's shape or size. Furthermore, we could take another bit of silly putty of the same mass as Feelix but differently shaped. Feelix won't be able to tell if he has his actual shape, the shape of the second bit of silly putty, or some other shape the silly putty could take. Now draw a border around two more regions. Call one region 'hand', another 'head', and a third 'foot', and imagine that Feelix moves in an amoeba-like manner. Feelix's hand can move nearer to his head than to his foot or nearer his foot than to his head, or it can be between the two. Feelix will not be able to encode that he has taken on these different positions: Without background

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[26] This poses difficulties for a recently proposed variant of the superficial schema, skin space, according to which, a superficial schema (skin space) is acquired by the stimulation of the skin without any additional input from prior representations of the body or other senses – including the other bodily senses – and this schema is sufficient for localizing and detecting the shape of stimulations on the skin's surface (Haggard et al. 2017; Cheng and Haggard 2018; Fardo et al. 2018; Cheng 2019).

information concerning the resting shape of the body and the range of motion of its parts, Feelix can't tell if increased tension registered by stretch detectors in the midlayer of the skin indicates that points on either side are brought closer together or farther apart. He will be able to encode information concerning the fact *that* he has moved but not *how* he has moved. Even if Feelix's hand were to touch his head, it would be indeterminate whether this was because they came into contact or because they were both touched by some other object(s).

Since Feelix's perceptual resources correspond with minimal touch, what goes for Feelix (with respect to sensory encoding) goes for minimal touch. The possible contributions of minimal touch, alone, to the formation of a body representation are limited to the continuity of the skin's surface.

3.2. Minimal Proprioception

Minimal proprioception involves mechanoreceptors that are found in the connective tissue of the musculoskeletal system: the fascia of the muscles (measuring tension and length), the tendons (measuring tension), and in the joint capsule and ligaments (measuring stretch and torsion, mainly at the extremes of the joint's range), and also in the midlayers of the skin (measuring skin stretch).[27]

The musculoskeletal mechanoreceptors cluster at the joints and lack the RF architecture seen with respect to tactile mechanoreceptors, so we shouldn't expect minimal proprioception to encode the continuity of the surface of the body, the position of the limbs and joints relative to one another, or the size and shape inter-joint body segments. The possible contributions of minimal proprioception to the acquisition (and updating) of the body schema will concern, at most, joint angles and body positions derived therefrom.

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[27] Each Golgi tendon organ has a transducer (sometimes more than one) that is sensitive to tension placed on the tendon (which connects a muscle to a bone). Muscle spindles contain two types of transducer, one which measures the contraction of muscle fibers and one which measures the rate of change of muscle contractions. Ruffini endings/SAII receptors in the skin (similar to Golgi tendon organs) track the degree and direction of skin stretch. Similar mechanoreceptors are found in the joints: Ruffini endings in joint capsules (which surround the joint and are filled with sinovial fluid) measure tension on membrane of the capsule. These are mostly sensitive at the ends of the joint's range of motion, but some respond to intermediate states. Ruffini endings are found in ligaments, with a similar function.

Skeletal muscles work in pairs – one muscle contracts to bend the joint a particular way, another to unbend it. Each muscle contains many muscles spindles with mechanoreceptors that encode length changes or tension in the muscle fibers. One of our algorithms can consider collections of these spindles to encode the overall tension/change in length within individual muscles. The tension on the tendons connecting the muscle to bone will be encoded by stretch-sensitive mechanoreceptors in the tendon organs found where the tendon connects to the muscle. Given the tracking of all muscle contractions relative to one another (via an algorithm) we might hope that information encoded by the receptors of two opposing pairs of muscles could determine information regarding joint angle (in the simple hinge-joint case) and, hence, that occurrent minimal proprioceptive stimulation would suffice for encoding joint angle. However, this information does *not* determine joint angle.

There are many reasons for this underdetermination, several of them widely recognized. For instance, proprioceptive information won't determine joint angle without background information concerning the size and weight of the limb segment moved (Craske et al., 1982; Gurfinkle and Levick, 1991; Longo, Azañòn, and Haggard, 2010; Longo and Haggard, 2010). Similarly for information concerning any resistance exerted by external impediments. The amount of tension/muscle contraction required to move a limb some amount will vary with all these features (There will be more tension on the ligaments when one bends the arm 15° while holding a 10 pound weight than while holding nothing.)

Other reasons for this underdetermination have received less attention. Consider a proprioceptive analog to Feelix, Bendji. Suppose that Bendji has a musculoskeletal system like ours, but his only sensory input comes from proprioceptors. When Bendji bends his knee, he will receive minimal proprioceptive input concerning the amount of contraction in the quadriceps and hamstrings and the amount of tension on the tendons attaching these muscles to the bone, the ligaments attaching the bones on either side of the joint together, the joint capsule, and the amount of stretch in the skin around the knee. But without background information concerning the resting angle of the joint, he will not be able to tell whether his knee is bent (as is normal for us) so that the lower leg and thigh are at a 90 degree angle or his knee is bent the same amount from a resting position where the lower leg extends forward 45° from straight (fig. 3).

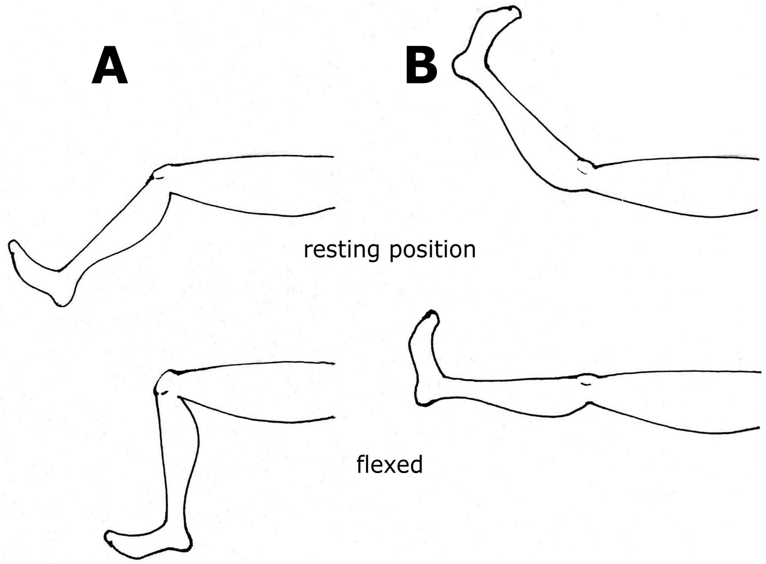

Fig. 3 (A) top: leg at normal resting position (equal tension on hamstrings and quadriceps); bottom: flexed 45° from resting to 90°. **(B)** top: leg at abnormal resting position; bottom: flexed 45° from resting to straight. Minimal proprioception does not distinguish A from B.

Even worse, though Bendji could learn which groups of transducers collaborate (including those of oppositional muscle pairings) via acquired background information about correlations among transducer activations from past stimulations, he can't *locate* them relative to one another because minimal proprioception doesn't enable acquisition of information about transducer *locations*. So far as I know, this has not been noticed before, but until the clusters of proprioceptors associated with oppositional pairings are located, Bendji can't tell that the contraction of one and stretching of the other is the result of bending a joint as opposed to a tug-of-war in which the two tendons are arranged in a straight line and attached to a floating ball in the center (rather than bone). If the muscle at the far end of one tendon contracts, pulling the ball toward it, the muscle spindles will encode a shortening of the muscle fibers while the spindles of the other will encode a lengthening, just as they would when bending a hinge joint. (Similarly for changes in tension, considered in conjunction with these changes in muscle fibre length.) Barring an appeal to innate background information – which we are presently trying to do without – Bendji must *learn* the spatial relationships between the transducers (e.g., whether the transducers of one muscle are situated as in a hinge joint or as in a tug-of-war relative to its oppositional partner).

We encountered a similar problem with respect to minimal touch/Feelix. There the RF architecture enabled learning the continuity of the skin's surface and adjacency relations among RFs, but there is no analogous RF architecture in minimal proprioception. So, Bendji is in an even worse position than Feelix with respect to learning the spatial distributions of his mechanoreceptors. What goes for Bendji goes for minimal proprioception, generally. In contrast to our everyday notion of proprioception, *minimal* proprioception does not encode the position of body parts relative to one another. It does not encode *any* postural information by itself. However, adding the resources of minimal touch to those of minimal proprioception will partially rectify the shortcomings of minimal proprioception (and vice versa).

3.3. Minimal Proprioception+Touch

We were left with two primary problems: (1) How to get information about the direction and distance of points on the skin's surface relative to one another given the limitations of minimal touch, and (2) how to encode joint angle given the limitations of minimal proprioception. These intersect at: (3) The problem of acquiring background information about the structure of the body to be combined with occurrent stimulation of the bodily senses to form the body schema.

It seems likely that (3) can be solved – at least in a rough fashion – by combining the resources of minimal proprioception and minimal touch. The idea is that a systematic exploration of the correlations of variations in stimulation of the mechanoreceptors of the musculoskeletal system (encoded by minimal proprioception) and those of the skin (encoded by minimal touch) will allow the acquisition of background information about the size and general location of the body parts relative to one another. This process is facilitated by the fact that minimal proprioception and minimal touch both take input from the stretch-sensitive mechanoreceptors (transducers) in the midlayer of the skin, thus ensuring that the two systems are spatially integrated.[28]

Tracking systematic correlations in proprioceptor and tactile receptor stimulations will allow us to learn the locations of proprioceptor groupings in relation to skin surfaces (given spatial integration) – i.e., we will be able to learn their spatial distribution relative to the skin and, therefore, learn that the groupings of coordinated proprioceptors cluster together. And we will be able to learn the location of these clusters relative to the joints, guaranteeing that oppositional pairings actually move a joint rather than engage in a tug-of-war.

To see how this would work, we can imagine a sequence of choreographed movements in which various body parts are moved along the surface of others. For instance, imagine pressing one's palms together at the body's midline. The various joint and muscle receptors of one arm will mirror the stimulation states of those of the other. Now raise the hands (still touching), by bending the elbows, until the inner forearms touch. The joint angles will be symmetrical and pressure on the forearms and hands will be (more or less) even. Bend the wrists back and slide the right forearm down along the left, until the wrist reaches the end of the elbow (fig. 4A). Then reset and perform the corresponding action with the left arm. In this way we verify (or disconfirm) that the forearms are the same length: If one forearm were

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[28] Shared transducers – in this case Ruffini endings (SAII) – pose no problem for the minimal senses approach provided that both minimal senses respond to the same class of energy and that the physical continuity of the receptor organs in which the transducers are embedded is secured. Both conditions are satisfied in this case: The transducers of minimal proprioception and touch both respond to mechanical energy, and the dermis is connected to the deep fascia of the muscles by the connective tissue of the superficial fascia/hypodermis – press or stretch the dermis, superficial fascia, or deep fascia and the others will be impacted too.

longer, portions of it not stimulated by the other at the start would come to be stimulated by it as the other began its slide. We can then run the forearms along each upper arm to verify that these, too, are the same length as one another.

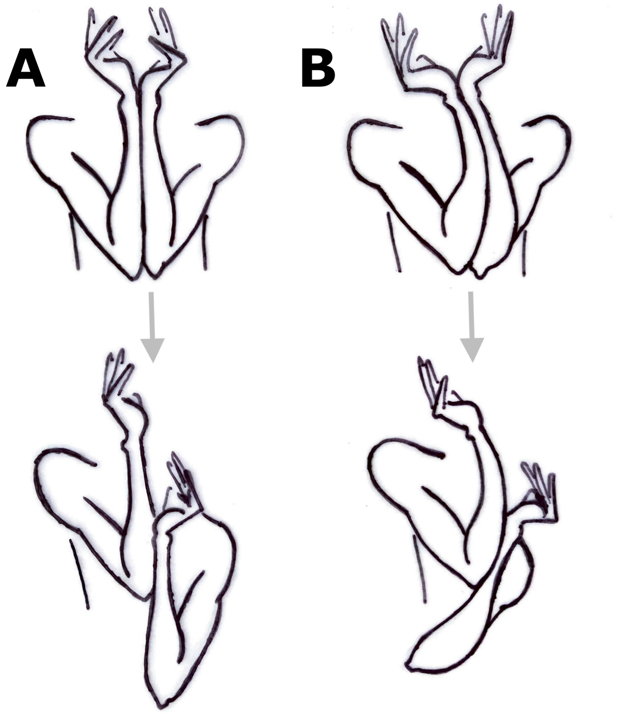

Fig. 4 (A) Straight forearms, straight upper arms, **(B)** curved forearms, straight upper arms. Change in the shoulder angle as one slides the left arm downward (lower image) from starting position (upper image) are greater for B than for A.

In the same way, we can establish that the forearms are (relatively) straight. Given uniform pressure applied at the joints (where the proprioceptors cluster), there will be (roughly) uniform pressure along the whole length of the segments brought into contact thereby *if these segments are straight*. If pressure falls off substantially, this indicates complementary curvature (or angles, depending on the rate of change in pressure along the relevant limbs). If there are regions without any pressure, then the limbs curve or bend away from one another. Our exploratory choreography can reinforce these results by comparing shoulder angles as each forearm slides down the other (fig. 4B). Similar exploratory movements would allow us to learn the size and shape of the hands. Continued explorations with the forearms and hands – once their relative sizes and shapes are learned – should be enough to establish the (rough) left/right symmetry of the body and the relative sizes and shapes of its parts.[29]

By integrating the results of our exploratory choreography, we can acquire the background information regarding the size, shape, arrangement, and range of motion of our body parts that is needed to encode present body position from occurrent stimulation of the minimal bodily senses, without further inputs from the other senses or innate endowments.[30] Furthermore, the exploratory choreography just is a regimented variant of the body babbling hypothesis. Given sufficient experience with more or less random movements (becoming less random over time), this same background information could be acquired. And the resources appealed to here are available to the fetus *in utero*. It is at least possible, therefore, that the body schema is acquired *in utero*.

3.4. Limitations

However, the body schema that can be acquired by minimal touch and minimal proprioception, alone, has shortcomings – particularly, with respect to scale and orientation – that must be overcome if it is to play its full role in action.

The first problem is that most of our actions depend on our ability to scale our body to the external world, which (for us) requires integrating bodily space with visual (and auditory) space. This is the scaling problem. For example, Felix (our left fielder from the introduction) can only know how high he must reach to catch the fly ball if he has a sense of how tall he is and how long his arm is relative to the spatial dimensions of the visual scene. It comes as no surprise that such scaling isn't available to minimal proprioception+touch, which does not have access to visual and auditory spaces.

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[29] Notice that this exploratory choreography depends on background information – e.g., that such-and-such joint angle + pressure, along with changes to both over time, determine the size and shape of limb segments. However, the rigidity of inter-joint limb segments and their constant size, relative to the rest of the body, will be guaranteed by the response (or, rather, the relative lack of response) of the stretch detectors in the skin.

[30] De Vignemont (2014) argues that *for the sighted* bodily awareness is partially constituted by vision because vision is less error prone than the bodily senses with respect to the metrical properties of the body. However, she does not deny that the blind can form a functional, if somewhat distorted, body representation (and so she doesn't deny that my choreography would do its job).

We might hope to solve the scaling problem by tracking changes in the body schema derived from minimal proprioception+touch as one moves through external space. However, to do so would require an implausibly accurate record of changes in the body's size through time to arrive at a stable, body-independent measurement of, e.g., its stride length. Furthermore, we couldn't distinguish between walking on solid, stationary ground and walking on a treadmill. That distinction will have to wait for vestibular input. And so, even if we could overcome the first difficulty, stride length won't determine distance in extra-bodily space.

Now for the orientation problem: Suppose a hybrid of Feelix and Bendji, call her FeeBee, whose sensory systems are limited to minimal touch and minimal proprioception, has acquired a body schema through exploratory movements (body babbling/our exploratory choreography). FeeBee could feel a tickle on her left arm and swat it away with her right arm, but she will not be able to know *that* it was her left arm that was tickled (or her right arm that did the swatting) from the standpoint of visually presented external space. The only spatial features that minimal proprioception+touch allows us to learn are spatial relations between parts of the body. And, where all we have access to are spatial relations internal to an object, we cannot determine whether we are presented with the object or its mirror image – or its front/back or top/bottom inversion – from the standpoint of some external space.[31] Minimal proprioception+touch, then, cannot orient the dimensions of bodily space to those of extra-bodily space, as visually or auditorily presented. But this is crucial for a body representation – such as the body schema – that is used to plan and execute actions with distal objects.

This is primarily a problem for creatures like us that need to integrate body space with the spatial frames of other senses. It will not matter to a creature with only bodily senses whether the touch is on its left arm *from the standpoint of visual space*.[32] It will not diminish its ability to swat away the touch on

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[31] The corresponding metaphysical fact has been well-known at least since Kant's introduction of his incongruent counterparts (1768). See Van Cleve and Frederick (1991) for a sampling of the philosophical work on this topic after Kant. The point here is epistemological, as we are concerned with the acquisition of the body schema.

[32] Such creatures could learn the orientation of bodily space to visual space through *cognitive* means. For instance, if the creature has spatial hearing, then it could orient bodily space to auditory space. If it then comes to understand

that arm with the hand connected to the other arm. There is no confusion about which arm is which in body space, just about which part of body space is on the left of external space (as visually or auditorily presented).

But there is one external dimension to which an action-guiding body representation must be oriented, even for a creature with only bodily senses; namely, up/down. The reason for this is that the influence of gravity does need to be accounted for when executing actions. It takes more force to lift something than to drop it. Orienting the body relative to external space – especially relative to gravity – is also necessary for a complete description of the current body posture: While we don't need to orient body space in external space to know the disposition of body parts relative to one another, we certainly *do* need to do so in order to distinguish, e.g., whether the pressure on one's back is due to the fact that one has backed up against a wall or that one is lying on the floor. And which of the situations we are in will certainly have implications for action. We will now consider the extent to which vestibular input can mitigate these problems.

4. Minimal Equilibrioception

The receptor organs of minimal equilibrioception are the vestibular labyrinths, found in the left and right inner ears. Each vestibular labyrinth comprises three semicircular canals attached to a central structure called the vestibule (fig. 5). The vestibule contains the otolithic organs – a saccule and an utricle.

The semicircular canals are composed of three loop-like structures, the anterior, posterior, and lateral canals, each oriented in a different plane. Each canal is filled with fluid that is disturbed by motions of the head in the plane to which it is oriented. Motion of this fluid stimulates hair cells (transducers) on a membrane allowing the detection of rotational acceleration in that plane. Algorithms

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that there is a visual space and that it corresponds to auditory space, it could know how its body is oriented from the standpoint of visual space. Indeed, this is likely to be true of congenitally blind humans.

considering the combined input of multiple canals (and otoliths) factor in determining rotation in intermediate planes.

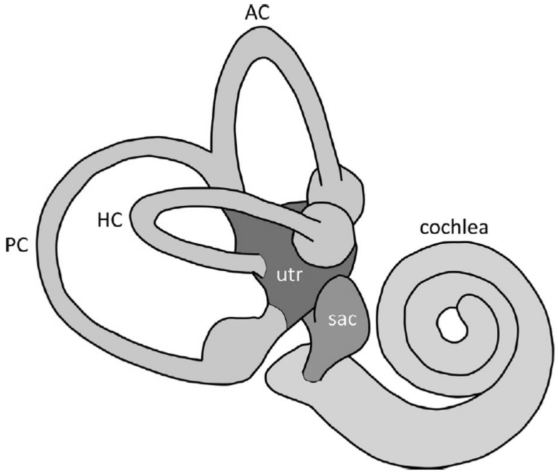

Fig. 5 *Illustration of the vestibular labyrinth*. Anterior canal (AC) and posterior canal (PC) respond to movement away from the center of the head in the plane to which they are oriented. The lateral (or horizontal) canal (HC) respond to horizontal rotations of the head. The utricle (utr) and saccule (sac) respond to linear acceleration/gravity. Diagram from Kingma and Van de Berg (2016, p. 4).

Hair cells on membranes within the otoliths (the saccule and the utricle) respond to acceleration. The utricle responds to acceleration in the horizontal plane and the saccules respond to acceleration in the vertical plane (relative to the head). Algorithms that compare input from the otolithic organs to input from the semicircular canals (which are only sensitive to rotational acceleration) can thereby determine the direction of gravitational force (based on deviations from uniform acceleration). Otolithic stimulation registers ‘gravity’s pull’ when there is no additional input indicating self-motion (e.g., from the semicircular canals or, leaving minimal equilibrioception, from proprioception and vision).[33] The otolithic stimulation Felix receives as he stands in left field between plays is due to gravity, that which he receives as he runs and jumps to catch a fly ball is due to his own motion (and its interaction with gravity).

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[33] Gravity is equivalent to uniform acceleration, and so what is strictly encoded, where psychologists and cognitive scientists speak of ‘detecting gravity’, is the deviation from uniform acceleration/cancelation of gravitational force introduced by an obstacle (in this case, the membranes of the otolithic organs).

It is clear that minimal equilibrioception won't encode any information about the spatial structure of the body on its own. Nor will it encode body-independent distances that might help solve the scaling problem. Given the mechanical function of the otolithic organs, once speed stabilizes we will stop receiving input. Therefore minimal equilibrioception can encode the duration of a changing rate of acceleration, but not the duration of movement (let alone speed or distance traveled).[34] To illustrate, as the speed of a car in which we are riding stabilizes, the otoliths cease to register our forward momentum and we no longer feel as though we are moving.

Minimal equilibrioception won't help with orientation, either. First, it does not have access to, and cannot acquire (on its own), the orientation of the left and right vestibular labyrinths relative to one another. As a result we cannot be sure that the left and right saccules respond to force exerted in the same plane. For example, if the saccules are oriented at a 30° angle relative to one another, then equal stimulation of the saccules would place the direction of gravitational pull by a stationary agent 15° off of what it would be were the saccules in line. Therefore, a given pairing of stimulations in the left and right saccules underdetermines which way is down. Similarly for the detection of front/back and left/right from otolithic stimulation.[35] The second problem is that minimal equilibrioception doesn't have access to, and cannot acquire, the orientation of the vestibular labyrinths in bodily space. So, even if there was a guarantee that, e.g., the saccules were oriented in the same plane, there is still no telling (from the standpoint of minimal equilibrioception) the angle at which that plane intersects bodily space.

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[34] The otolithic membrane is heavier than the surrounding structures of the otolithic organs and so responds more slowly to acceleration, but shortly after stabilization, the membrane will catch up to the rest of the organ and stop responding.

[35] There is a corresponding problem for the orientation of the semicircular canals and vestibule to one another within a single vestibular labyrinth, as well. (As we will see below, this orientation could be acquired and so there is no need – according to the approach we are taking here – to appeal to innate information about this orientation.)

The upshot is that minimal equilibrioception merely encodes the presence of forces in indeterminate directions. But it *can* make important contributions to the acquisition of body representations once it is combined with the other minimal bodily senses.[36]

4.1. Minimal Proprioception+Touch+Equilibrioception: Orientation

Though minimal equilibrioception cannot encode the *direction* of gravity, it could encode the law-like covariation of activation states of the vestibular labyrinths. And, by considering the total stimulation of the minimal bodily senses, we could learn how these law-like regularities in vestibular activation correlate with bodily movements tracked by the rudimentary body schema derived from minimal proprioception and minimal touch. For example, as the fetus rotates, it will receive tactile stimulation of the body parts that contact the uterine wall that will progress in the opposite direction of the fetus's movement. This tactile stimulation will correlate in a law-like way with stimulation of the mechanoreceptors in the semicircular canals (and registration of the position of the head relative to the rest of the body). This would allow the fetus to acquire background information orienting minimal equilibrioceptive stimulation within bodily space.

This, in turn, would enable the encoding of the orientation of one dimension of bodily space in (visually presented) external space, *but only this one dimension* – namely, up/down. This is so because gravity provides an asymmetry between up and down that allows them to be differentiated from one another. There is no analogous asymmetry for left/right or front/back. While we will be able to match forward momentum with momentum in the direction of the front of the body – just as we will leftward motion with one side of the body – that will not determine which direction is forward and which is back in visually or auditorily presented *body-independent space* any more than it will which is left and which is right.

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[36] That vestibular input primarily augments the other senses should be unsurprising given the fact that there is no dedicated portion of the cortex for processing vestibular input but we do see vestibular inputs routed to the regions of cortex traditionally treated as dedicated to other senses (somatosensory cortex, motor cortex, visual cortex).

Ultimately, *each dimension* of bodily space represented in the body schema must be oriented with respect to (objects presented in) the other spatial frames if it is to play is proposed role in action. It is unsurprising that we cannot achieve such a complete orientation with visual and auditory (and perhaps other) spaces without visual and auditory (and perhaps other) input.

4.2. Minimal Proprioception+Touch+Equilibrioception: Scale

Despite the fact that it won't enable encoding of the *direction* of travel in extra-bodily space, integrating minimal equilibrioception with a body schema derived from minimal touch+proprioception and occurrent minimal proprioceptive stimulation could allow us to encode *that we are moving* through external space.

For example, by integrating changes in body shape associated with locomotion that are tracked in the rudimentary body schema (via minimal proprioceptive input), pressure on the soles of the feet as they push against the ground (thanks to minimal touch), and stimulation of the saccules as we move forward (via minimal equilibrioception), we could encode that we are walking through external space, as opposed to walking on a treadmill.[37] However, this will not be enough to solve the scaling problem. The reasons here are the same as those given in §3.4:

Scaling the body to a body-independent space with only a body-based frame of reference, where (a) bodies change over time and (b) the spatial relationships between the individual transducers of each bodily sense need to be learned, would require an implausibly detailed record of past body representations updated with frequent recourse to something like our exploratory choreography.[38] Nothing contributed by minimal equilibrioception changes this – not even the fact that we can now encode the duration of travel. If the size of one's strides aren't already scaled to external space, the fact that you walked for so many

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[37] The response of the otolithic organs to linear acceleration is transient – the response of the organs subsides shortly after the speed stabilizes (see n.34). When we stop moving or slow down, we will get activation in the opposite direction of travel, due to inertia. These changes are law-governed and will correlate with bodily movements associated with locomotion, so we will (diachronically) encode duration of movement.

[38] And some independent assurance that the objects against which we measure ourselves remain a constant size/are in fact the same objects at each instance of measurement.

minutes, taking such-and-such a number of strides, while experiencing some particular otolithic stimulation, won't determine a body space-independent distance travelled.

Resolving this indeterminacy of worldly distance will require input from elsewhere. In particular, it will require input that allows us to scale body space to an independently presented extra-bodily space. This is not one of the possible contributions of body representations acquired just through the minimal bodily senses.

5. Implications and Future Directions

5.1. The Origins of the Body Schema

A fairly substantial body schema *could* be acquired via perceptual learning *in utero* – at least this cannot be ruled out on conceptual grounds. But this is not a *fully mature* body schema. The scale problem and aspects of the orientation problem remain unsolved, so long as we are restricted to sensory input from the minimal bodily senses. This limits the sort of imitation that the present-at-birth body schema could support, should imitation results be vindicated. For instance, in Meltzoff and Moore (1989) conducted a study that purports to show imitation in clockwise head rotations (as opposed counterclockwise rotations, which were taken to be indicative of tracking the experimenter's head movements), in infants no older that 72 hours. If the body schema results solely from body babbling without any visual or auditory support, the infants should not be able to corelate visually perceived clockwise movements of others' heads with proprioceptive clockwise movements of their own heads because the body schema has not been oriented with respect to visual space.

While *in utero* visual stimulation is highly limited, it remains possible that the fetus has sufficient experience with shadows cast by a moving body part passing between the fetus's eyes and a light source strong enough to penetrate the womb to solve the orientation problem on the basis of perceptual learning. Similarly, though *in utero* auditory input is restricted to low-frequency components that are harder to localize, sufficient experience with alterations in auditory stimulation related to fetal movements might allow perceptual learning to solve the orientation problem with respect to auditory space.[39] This suggests that further research is needed on the potential role for vision and audition in perceptual learning *in utero*.

Should such studies show that *in utero* visual and auditory input is insufficient to solve the orientation problem *and* should imitation results requiring orientation to visual or auditory space be vindicated, then we can conclude that there must be some innate endowment involved in solving the orientation problem (*in utero*).[40] Notice, though, that this innate orientation mechanism – which need only orient the body schema in extra-bodily space – falls far short of the innate endowments posited by Gallagher and colleagues, which include innate representations of body parts.

Further study is also needed to determine how reliable the imitation results are. These studies should test a variety of orientation-dependent tasks. (Here we circle back to the evaluation of present-at-birth accounts, relative to the traditional view, in addition to helping clarify the role of innate endowments and perceptual learning *in utero*.) Relatedly, studies on non-imitation-based activities – preferably free of the confounds such as social motivation – requiring orientation should be pursued. Similar studies can (and should) be directed towards the origins of the solution to the scaling problem, which seems less likely to have an *in utero* perceptual learning-based solution.

Note, too, that my account has not addressed constraints on fetal movements imposed by either developmental stage or the by the uterine environment, itself. Further study on these issues will be crucial for assessing the extent to which *in utero* body babbling supports the formation of the body schema.[41] The account I have provided here lays the groundwork for such studies by specifying how to link particular movements to informational contributions to the body schema.

5.2. The Individuation of Body Representations

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[39] While the neural mechanisms responding to binaural auditory discrepancies are fully formed prior to birth, it remains probable that a period of learning (postnatally) is required to use binaural cues for sound localization (Muir et al., 1979; Muir et al., 1989; Clifton et al., 1981; Muir and Hains 2004).

[40] Unless it can be shown that 72 hours is sufficient for the acquisition of a solution to the orientation problem from sensory inputs.

[41] Hayat and Rutherford (2018) for an MRI protocol for studying fetal movements that accommodates these issues.

The minimal bodily senses approach also has promise for addressing the broader question of individuation of the (increasingly large number of) body representations that have been proposed. In a recent review article, Longo (2016) offers a (non-exhaustive) list of six distinct candidates. As Longo classifies and describes them, these are:

- *body image*: a conscious representation of the size, shape, and composition of the body
- *body schema*: a dynamic representation of the disposition of body parts relative to one another
- *superficial schema*: a representation used for localizing stimulation on the body's surface (the skin)
- *body model*: a representation of the metrical properties of the body subserving perception
- *semantic body representation*: a representation of conceptual information concerning the body
- *structural body description*: a consciously accessible cognitive representation of the body's structure used in making judgments about the spatial relationship of body parts to one another

There is little agreement on the exact number of distinct body representations in the brain, their functions, and the extent to which the mechanisms implementing them overlap. The least controversial of these, along with the body schema, is the body image. Even here, there have been challenges both to the distinctness of the body image from the body schema and to the unity of the body image itself.

Evidence for the distinctness of the body schema and the body image derives from dissociations exhibited in bodily disorders such as anorexia nervosa (AN) and Alice in Wonderland syndrome (AIW). AN patients represent themselves as weighing more than they actually do, implicating the body image. However, they are *not* impaired in their movements, as they would be if the body schema were affected. AIW is generally characterized as feeling as though one's legs are shorter than they are, though there is (usually) no impairment in actions taken with the legs – e.g., walking. This also suggests that representations supporting the perception of and judgments about the body (body image) are distinct from those tracking the body's position for use in action planning and guidance (body schema).

Recent work calls into question the extent of these dissociations. Pitron and De Vignemont (2017) cite first person reports of AIW to demonstrate that, in some cases, there *are* impairments of action corresponding to the misperception of body size. This leads them to propose the 'co-construction model' on which the body schema – though distinct from those of the body image – can influence the updating of the body image, and vice versa, leading to mirrored deficits in both body representations. Cases of complete dissociation are explained by positing an impairment of the mechanism that implements the cross-representation updating.[42]

Recent empirical work also suggests that the body image might not be best construed as a single representation. In a seminal paper Schwoebel and Coslett (2005) divide the traditional body image into a *structural body description* – a representation of the boundaries and proximity relations of body parts, which they took to be derived from visual input – and the body image, proper – which houses conceptual and affective contents pertaining to the body (e.g., associations of tools with the body parts required to use them).[43] Schwoebel and Coslett located the body schema in the posterior parietal cortex (PPC) and the body image and structural body description in (different parts of) the temporal lobe. More recent work on body image disturbances in AN has clarified and extended our understanding of the brain areas contributing to the body image – e.g., the insula, which is thought to contribute affective components to the body image (Mohr et al., 2010; Lee et al., 2014; Araujo et al, 2015; Ehrlich et al., 2015; Via et al., 2018).

Kanayama and Hiromitsu (2021) suggest that the structural body description is derived from the bodily senses-derived body schema and visual input pertaining to the body traditionally associated with the body image (2021, p. 141). As with the co-construction model, this suggests that one body representation might well include or draw on (a part of) another. If that is correct, understanding the

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[42] See Gadsby (2018) for criticisms of the co-construction model. See Pitron, Alsmith, and de Vignemont (2018) for a partial – to this reader's eye – response.

[43] Notice that this characterization lumps the body image, proper, together with what Longo calls the semantic body representation. Such lack of agreement about labels for putative body representations is common in this literature.

acquisition of one body representation (e.g., the body schema) can advance our understanding of others (e.g., the structural body description, insofar as it builds upon the schema).

Furthermore, the recent work on AN – as a disorder of the body image – cited above suggests that body representations are constituted by distributed, probably overlapping, networks rather than isolated brain regions. Distinct portions of these networks seem to correspond to different sorts of information pertaining to the body (perceptual, affective, conceptual) from different sources (e.g., bodily senses, vision) – information that is relevant to a wide range of functions served by putative body representations (e.g., input from the bodily senses, information pertaining to body topography or body metrics, etc.). This speaks against treating the putative body representations as distinct, functionally demarcated entities.

Indeed, looking back at Longo's list, we can see that the differences between many of these putative body representations are quite subtle: The body image differs from the body model primarily in that the former is consciously accessible while the latter functions as a subpersonal basis for locating bodily sensations and supporting tactile perception. The body model differs from the structural body description in that the latter is the basis for *judgments* concerning the spatial relations between body parts, which can come apart from the *perception* of these relations enabled by the body model and in that the former is not necessarily consciously accessible. And the structural body image differs from the body image (on Longo's characterization) in that it does not contain content concerning the material composition of the body, only a representation of its spatial structure.

Given the subtle differences between these representations and the overlaps in the sort of information they must encode, along with the distributed nature of body representations in the brain, it seems likely that there is considerable overlap in the mechanisms implementing these (putatively) distinct representations or even that some of them are merely different functional elaborations on a shared underlying representation.[44]

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[44] This points to a more general problem: functional shortcomings found in a given bodily disorder might be caused by damage to a body representation that specifically supports that function *or* by damage to a mechanism that accesses a prior, more general body representation supporting many functions. Similarly, different spatial resolutions might result from the functional requirements of a mechanism accessing an underlying representation of

Nevertheless, these representations *are* often treated as discrete, self-contained constructs. The evidence for this treatment – as with the body schema and body image – comes from dissociations. But the range of these dissociations is vast and can be interpreted to be consistent with both many discrete body representations serving different functions and a complex body representation network including mechanisms that draw on shared representations to perform different functions. Continuing to treat these putative body representations as discrete functional units threatens to obscure the actual overlaps and interactions within the overall body representation network. As Ho and Lenggenhager put it, speaking of AN: "By using the body image as a unitary construct, and not considering the perceptual, affective, and cognitive subcomponents, it is more difficult to draw valid conclusions surrounding the anatomical signatures of AN" (2021, p. 277).

If we are to heed Ho and Lenggenhager's warning – as we should – then we should consider each putative body representation in light of the potential perceptual, conceptual, and affective contributions to the performance of its assigned function(s). This is where the minimal bodily senses approach can help. All these putative representations will be updated on perceptual input from the bodily senses – either directly or through an intervening body representation. Therefore, everything I've said about the possible contributions of the minimal bodily senses to the acquisition of the body schema applies to the possibility of acquiring (aspects of) the other body representations from sensory input *in utero*. And we can identify functional shortcomings relative to putative body representations in the same way that we identified the orientation and scale problems, above. Furthermore, given our relatively good understanding of early perceptual processing, and its associated pathways, clarifying the perceptual contributions to the formation and updating of body representations lays the groundwork for understanding how other inputs interact with perceptual components to form and update the complete body representation network.

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body size and shape. For instance, processing loads can be reduced by mechanisms that need less fine-grained information by treating a range of values as equivalent. See De Vignemont (2007; 2018, ch. 8) and Holmes and Spence (2006) for a thorough discussion of the shortcomings of current empirical approaches.

More generally, the fine-grained analysis of perceptual processing required by my approach – with its careful build up from occurrent stimulation through subsequent stages of processing – provides guidance on where to look for the mechanisms implementing these (fine-grained) processing functions: We target functions of interest (e.g., those involved in orienting body space to extra-bodily space) and study brain activity related to that function (e.g., by fMRI scans of individuals in the process of adapting to inverting lenses) in light of what we already know about the relevant perceptual processing. We can also study brain activity in regions antecedently thought to be involved in particular body representations with an eye toward the way these areas link up with perceptual processing. This will tell us what fine-grained processing functions they might be contributing to, given their observed activity in response to sensory inputs/experimental task performance. As our understanding of other sorts of inputs (e.g. affective) catch up to our understanding of perceptual processing, we can make similar inferences about the roles their associated brain areas are playing in the body representation system.[45]

This, in turn, informs us about the maximum degree of overlap between the components of mechanism implementing putative body representations. As such, this approach is better suited to understanding the nature of body representations in the brain than the unitary constructs approach. If the body representation system is a network of overlapping representations with shared mechanisms/contents, then the unitary construct approach obscures this fact. If the body representation system is, in fact, a collection of discrete, functionally differentiated body representations, then the approach I am urging will reveal this. Furthermore, a clearer picture of the neural mechanisms implementing body representations will help us to better understand the disorders of body representations that have been the source of so much theorizing about body representations, hopefully leading to therapeutic advances.

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[45] This will also advance our understanding of other body-involving spatial representations – e.g., peripersonal space, the space immediately surrounding the surface of the body which is processed by input from the body schema and the exteroceptive senses (including vision and audition). As with other body-based representations, there is debate over the number of representations of such peripersonal spaces (de Vignemont 2018; Vagnoni and Longo 2019).

In short: Clarifying what the stimulation of the bodily senses can contribute to the formation of body representations better positions us to untangle the web of issues surrounding the origins and individuation of body representations in the brain with both theoretical and practical benefits. It is the first step in understanding how we go from Feelix to Felix.

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