# 11

# DISTINGUISHING BODY REPRESENTATIONS

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## 11.1 Introduction

Early researchers in body representation were clinicians who examined a wide variety of individuals with perceptual and cognitive deficits (see Coslett, this volume, for a review). These observations led to the identification of either behavioral syndromes (e.g. Gerstmann's syndrome) or early proposals of the existence of various types of body representations. In the most influential account, Head & Holmes (1911) presented eighteen case studies who were tested on an extensive battery, including assessment of tactile thresholds using von Frey hairs, tactile localization, position sense, two point discrimination, weight judgments, haptic identification, and other tasks. Using these observations, Head and Holmes identified two major schemata – a postural schema which represents changes in perceived body position, and a separate schema involved in localizing sensations to specific locations on the body surface itself, often called the "superficial schema."[1] In the late nineteenth and early twentieth centuries, other researchers proposed similar distinctions which varied in the classification of these schemata (Pick, 1915; Schilder, 1923/2013; Munk, 1890).

After the early work of Head and Holmes (1911) and others, the cognitive revolution led to changes and increased formalization regarding the interpretation of evidence from brain-damaged individuals. Going beyond syndromic classification and taxonomic categorization, the field of cognitive neuropsychology used evidence from brain-damaged individuals to develop and formalize information processing accounts which allowed for the specification of functional architectures for various cognitive processes (e.g., Caramazza, 1986; Shallice, 1988). While this approach was quite successful in developing influential processing accounts in memory, language, attention and other cognitive domains, limited progress has been made in developing such models for body representations. In this chapter, I will provide a brief overview of recent accounts of body representations, focusing on how evidence from brain-damaged individuals has contributed to these accounts. I will then discuss potential critiques of past approaches to understanding body representations, with a particular focus on the limits of taxonomic explanations. I will then conclude with some suggestions on moving forward towards a more substantive understanding of body representations.

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## 11.2 Development of taxonomic body representation accounts

Modern accounts have used task dissociation logic to identify the existence of multiple body representations. A single dissociation is when an individual with brain damage demonstrates a deficit on task A but not task B. Although one could infer that task A and task B involve different cognitive processes, there are other explanations that do not need to postulate separate representations; including task-resource and task-demand artifacts (Shallice, 1988). Based on this, strong evidence for representational dissociations come from double dissociations – two single dissociations in which one participant is impaired at task A but not task B, while the other is impaired at task B but not task A. Double dissociation logic has been the gold standard for identifying functional dissociations in cognitive neuropsychological studies and has guided the development of body representation models.

Paillard (1999) utilized evidence from individuals with either central or peripheral deafferentation to propose a dyadic taxonomy (de Vignemont, 2010) between body schema and body image. Paillard's account, strongly influenced by what/where processing distinctions proposed at the time for the visual system (Mishkin and Ungerleider, 1982), proposed a similar dichotomy for representing the body in space. Utilizing earlier terminology, they defined the *body schema* as a proprioceptively dominant representation of body position in space ("where"), while the *body image* is a visually dominant representation used for perceptual information regarding body features ("what"). In support of this dissociation, they review the case of R.S. (originally reported in Paillard et al., 1983) who demonstrated severe right-sided hemianesthesia (inability to feel touch on one side of the body) subsequent to left parietal lobe damage but could still make localization judgments to these tactile stimuli. This performance was contrasted with the well-studied individual G.L. who developed demyelination (damage to the myelin sheath that results in impaired signal conduction) of the large nerve fibers that transmit tactile and proprioceptive information to the brain (peripheral sensory neuropathy). She demonstrated a complete loss of touch and proprioception but was able to detect thermal and pain sensation (Paillard, 1999). Utilizing cold or pinprick stimuli, she was able to verbally identify where she was touched and point to the location on a viewed picture of the hand. However, given her profound proprioceptive deficit, she was unable to accurately point towards the stimulus location when blindfolded, especially if the stimulus was followed by passive movement of the hand. These cases taken together provided evidence for a double dissociation between tactile detection (impaired in G.L., intact in R.S.) and tactile localization (intact in G.L, impaired in R.S.). Along with this double dissociation between tactile detection and localization, other aspects of their performance suggested additional characteristics that were tied to the body schema and body image. R.S.'s ability to localize without conscious perception – numbsense – suggested that the body schema mediated unconscious processing. Paillard (1999) claimed that G.L.'s ability to localize touch on the skin surface was mediated by an intact body image, with her inability to represent body position in space without vision being related to an impaired body schema. Given her conscious awareness of this deficit, the body image was tied to conscious processing. This and similar double dissociations involving brain-damaged individuals and those with peripheral neuropathy have led to similar divisions, though the focus and dividing lines between body schema and body image vary according to different accounts (see de Vignemont, 2010 for a review).

Dijkerman and de Haan (2007) also used dissociations observed in vision to inspire categorization of streams of body representational processing. Mirroring how the what/where hypothesis of Mishkin and Ungerleider (1982) developed into the vision for action/vision for perception model of Goodale and Milner (1992), they proposed the existence of a dorsal "somatosensation for action" system (body schema), and a more ventral "somatosensation for perception" (body image) system. Along with a change from a what/where to a perception/action account, Dijkerman and de Haan also related these processes to specific neural substrates. The neural pathways of both systems diverge after secondary somatosensory cortex, with the action stream projecting to superior parietal cortex (Brodmann areas 5 and 7), whereas the perception stream projects to the intraparietal sulcus and terminates in the posterior insula. Their account uses similar evidence as Paillard (1999), e.g., highlighting the dissociation between individuals with numbsense (Figure 2) and G.L.'s performance on localizing cold stimuli (Figure 3) in support of their dissociation.

Additional evidence from case studies led to the development of a triadic taxonomy of body representations (Sirigu et al., 1991; Schwoebel and Coslett, 2005). This distinction was driven, in part, by evidence from autotopagnosia. Individuals with this deficit perform well on tasks generally related to the body/postural schema (e.g., localizing objects on the body surface, grasp aperture when reaching to objects) and demonstrate semantic knowledge about the body (e.g., associating clothing to body parts). However, these individuals demonstrate deficits in tasks that involve knowledge of body part boundaries and the relationship between body parts, such as pointing to visually presented body parts or matching body parts viewed from different angles. In Schwoebel and Coslett (2005), the body schema remained relatively unchanged from previous definitions – an online representation of the body in space used for action. To account for autotopagnosia, they proposed the *body structural description*, a primarily visual, topographic representation of the body used for defining body parts and relationships. In this account, the *body image* differs substantially from prior definitions. Instead of being related to perceptual systems, Schwoebel and Coslett (2005) conceptualized this as a lexical-semantic representation of the body, as individuals have been reported with selective deficits in comprehension of body part names with other categories intact (Suzuki et al., 1997) with others demonstrating the opposite pattern (Coslett et al., 2002). The former case did not demonstrate autotopagnosia, providing evidence for a dissociation between the *body structural description* and *body image* as conceptualized by Schwoebel & Coslett (see Schwoebel and Coslett, 2005 for additional evidence for these distinctions from a larger cohort of brain-damaged individuals).

## 11.3 Issues with taxonomic body representation accounts

The study of body representations has developed over time, first relying on performance from case studies to identify syndromes and general categories. While interesting and informative, these taxonomic accounts suffer from a number of issues. First, taxonomic distinctions provide broad categories that, without further parcellation, are limited in their explanatory power. In their critique of the body schema concept, Poeck and Orgass (1971) wrote:

> Under the heading of body schema disturbances, there have been grouped together a great number of very heterogenous symptoms. … The subsequent expansion of the doctrine to cover also such unrelated phenomena as phantoms, anosognosia, neglect, paroxysmal disturbances of body experience, and even "pain asymbolia," heautoscopy and later on psychiatric and neurotic conditions (d. Frederiks, 1969) had the consequence that the terms "body schema" and "body schema disturbances" eventually lost any unequivocal meaning. Therefore, the concept of the body schema has, in our opinion, become practically useless.
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> *p. 274*

A similar critique was put forth by de Vignemont (2010), stating "If a putative disruption of the body image can lead to phenomena as diverse as Cotard syndrome (i.e. you believe your body is dead and rotting) and finger agnosia (i.e. you cannot name your fingers), then there is a risk of making the concept of a body image empty of meaning and explanatory power."

Second, it is not clear that the primary evidence that underpins the dyadic dissociation – individuals who can localize touch without being able to detect touch – is particularly strong. Participants with numbsense who have impaired detection but intact localization are rare but foundational for the double dissociation that underlies the dyadic body schema/body image distinction. A major concern regarding examinations of individuals with numbsense is the nature of the tasks. In the case of R.S. (Paillard, Michel and Stelmach, 1983), tactile detection was tested using an esthesiometer in which she would respond as to whether she felt pressure. Her detection performance across sessions was inconsistent, as she was unable to detect stimuli in the first session, but could do so vaguely (as an "event") in subsequent sessions. On a tactile localization task, she was presented with both tactile stimulus and catch trials in which no stimulus was presented. Although she made localization judgments on 48/54 trials, she never (0/10) attempted a localization judgment on a catch trial. R.S. was not first asked to detect, then localize, but were instead asked to make a localization judgment on a verbal cue. Given that she was not asked to first detect, then localize the stimulus, it is plausible that she would have consciously detected stimuli she made a localization judgment towards, and not detected stimuli on trials with no pointing response. Her lack of responses on catch trials suggests that her localization judgment was mediated by some ability to consciously detect the stimulus.

Third is the lack of consensus regarding exactly how these representations are delineated. Dyadic distinctions are often based on a primary boundary that varies depending on the account. Both Paillard (1999) and Dijkermann and de Haan (2007) divide based on function, whereas others accounts separate based on conscious versus unconscious processing (Gallagher, 1986, 2005) or short-term versus long-term processing (O'Shaughnessy, 1995). Depending on the account, the same deficit can be categorized under different taxonomies. For example, personal neglect (inability to attend to one side of body) and apraxia (inability to perform skilled, learned movements) have been categorized as body schema deficits by some (Coslett, 1998; Schwoebel and Coslett, 2005) and as body image deficits by others (Gallagher, 1995; Goldenberg, 1995). For a discussion of these issues, see de Vignemont (2010) and Kammers and colleagues (2010). Even with these well-known and well-documented issues of inconsistent usage and application of these terms, many empirical findings that are explained by invoking some general involvement of the "body schema" or "body image."[2] This may be due to a lack of consensus regarding terminology along with difficulty in situating new results in a theoretical landscape filled with vague or inconsistently defined concepts. It is easier to say that new findings relate to an overgeneralized "body schema" or "body image," which continues to perpetuate underspecified usage of the term.

What can be done? One possibility is to give up on representation entirely. Another path is continuing to dissect body representations based on new dimensions, whether it be a "working body schema" and "protective body schema" (de Vignemont et al., 2021), local versus global body schemata, or adding additional taxonomic boundaries. Although potentially promising, a concern is that these types of accounts focus more on categorization, and less on developing information-processing models that are at the core of cognitive science. Instead, using an example from the development of language research, I propose that the key to making progress is developing information processing models for body representation. Classic observations from brain-damaged individuals have provided evidence for a dissociation between language production (Broca's aphasia) and language comprehension (Broca, 1861; Wernicke, 1874).

Continued research with brain-damaged individuals have found a host of other dissociations. To use performance on picture naming as an example, there have been dissociations identified for nouns and verbs (Damasio and Tranel, 1993), animals (Hillis and Caramazza, 1991), fruits and vegetables (Hart et al., 1985; Crutch and Warrington, 2003), proper names (Miceli et al., 2000; Semenza and Zettin, 1989), and more. Although interesting, being limited to taxonomy provides a host of categories and dissociations, but not an overarching model of lexical processing.

A common assumption is that neuropsychological evidence only contributes to the understanding of normal cognition by way of task dissociation logic (see McCloskey, 2003 for an in-depth discussion). While important, neuropsychological studies can also use evidence from error patterns along with other sources to develop richer, more explanatory cognitive models (Medina and Coslett, 2016). Using lexical processing as an example, meaningful developments were made from analyzing error patterns (both from brain-damaged individuals and the neurologically intact) to develop computationally explicit processing models that could explain both healthy and impaired performance on a particular task (Levelt et al., 1999; Dell, 1986). Stating that someone has a body schema impairment is similar to noting an impairment in "language production." While performance may be related to this general category, this provides little progress towards developing testable, meaningful accounts of processes related to body representation. This can be achieved by taking steps to develop more explicit processing models of different aspects of body representations. More recently, evidence from human behavioral studies, non-human primate neural recording studies, and neuropsychological case studies have been integrated to develop accounts that are more akin to cognitive processing models as opposed to taxonomic categorization. One such example is in our understanding of the "body schema" with regard to tactile processing.

## 11.4 Developing processing models: Body schema and touch

A question typically under the aegis of body schema accounts is understanding how information starting from stimulation of mechanoreceptors on the skin surface is transformed into the qualia of feeling touch at a particular location on the body. Different accounts have been proposed regarding how sensory information is processed for detection and localization. In parallel processing models (e.g. Paillard, 1999), information for detection and localization are processed independently. In serial models, information is first processed to make a judgment regarding detection, and is then passed to a second, separable process used for tactile localization. To test these potential models, Harris and colleagues (2004) presented neurologically intact participants with a brief, masked tactile stimulus to one of four fingers, and could either detect (yes/no task) or localize the stimulus. Participants performed significantly above chance on localization trials in which they did not detect the stimulus, seemingly consistent with accounts demonstrating independence between detection and localization. However, a second possible explanation is that participants utilized different criterion for each task. When presented with a detection task, participants could be more conservative for judging whether a stimulus is present; whereas they could be more liberal when using that same information to localize touch on a finger. Comparing the experimental data to simulation based on three types of processing models (serial, parallel, and one shared detection/localization process), the results were most consistent with a serial model (see also Harris et al., 2006). Differing criterion for tactile detection based on task or setting may also explain performance of individuals with numbtouch, who may use a more conservative criterion for tactile detection versus a more liberal criterion for deciding on a localization judgment.

Next, how is information processed leading to a percept on a location on the skin surface? Early accounts proposed a fixed mapping between activation for a neural pathway (including neurons in a cortical map) and the location of sensation (labelled-line hypothesis; see Rose, 1999 for a discussion of the history of this topic). However, this is unlikely given evidence from individuals with damage to primary somatosensory cortex (S1) and differential stimulation. If this hypothesis were correct, then damage to a region of S1 would result in complete loss of sensation for that area. Although hemianaesthesia can occur after large lesions (Sterzi et al., 1993), there are multiple cases of individuals who can still detect touch after damage to primary somatosensory cortex[3] (Birznieks et al., 2012; Halligan et al., 1995; Rapp et al., 2002). Furthermore, differential stimulation of the fingertips leads to an expansion of the fingertip representation in S1 (Jenkins and Merzenich, 1987), but this expansion does not lead to increased mislocalization (e.g., single-finger Braille readers; Sterr et al., 1998). These and other results provide evidence that there is not a strict one-to-one mapping between activity in specific somatosensory neurons and the qualia of sensation at a particular location on the skin surface, thereby necessitating a secondary representation involved in such a mapping. From this and other evidence, it was proposed that information from early somatosensory representations (e.g., a superficial schema) is likely mapped to representations of the size and shape of the body (called the *body form* representation in Medina and Coslett, 2010; or the *model of body size and shape* in Longo, Azanon, and Haggard, 2010).

Based on hypotheses regarding mapping between earlier somatosensory representations and representations of body size and shape, one can generate testable predictions regarding how various manipulations can influence perceptual processes. As commonly shown in sensation and perception textbooks, there are large differences in tactile acuity on different locations of the skin surface (Weinstein, 1968; Mancini et al., 2014). These performance differences are due to receptor density on the skin surface and representational territory in primary somatosensory cortex. Taylor-Clarke, Jacobsen, and Haggard (2004) noted that although the ratio of cortical representation in S1 to skin surface varies for different body parts, we still experience size constancy suggesting some rescaling from these early representations to a representation of body size and shape. As part of this rescaling process, distortions should remain such that tactile distance judgments would be overestimated for skin regions with a larger cortical representation to skin surface ratio. When participants in Taylor-Clarke, Jacobsen, and Haggard (2004) were presented with tactile distances of the same length to the finger (higher ratio) versus the forearm (lower ratio) and ask to judge which was longer, they were significantly more likely to choose the finger, consistent with their predictions. Another prediction from this account is that changes in perceived body size would also alter tactile distance judgments for unseen stimuli, such that experiencing a body part as larger would also result in an increase in the perceived length of tactile distances on this body part. These predictions have been borne out, both with visually (Taylor-Clarke et al., 2004) and proprioceptively (de Vignemont et al., 2005) mediated changes in perceived body size. How this representation of body size and shape is instantiated or maintained is unknown, although immediate changes in perceived body size after local anesthesia suggest a process in which it is maintained by tonic neural activity (Paqueron et al., 2003; Türker et al., 2005).

Information about the location of a tactile stimulus can be represented on a particular location on the skin surface – i.e., in a somatotopic frame of reference. Although useful, this is insufficient for representing touch on our bodies and our world. Repeating an often used example, having detailed knowledge that a mosquito has landed on the dorsal side of the medial segment of your left ring finger is not informative for swatting the insect without some knowledge of the configuration of your body relative to your other body parts and the external environment. This representation has been termed the *postural schema* (Head and Holmes, 1911; Longo et al., 2010) or a postural representation (Medina and Coslett, 2010). More recent accounts have worked towards not just classifying this type of representation, but developing a better understanding of the nature of this representation, including how information is transformed and represented. For example, any spatial representation must have a frame of reference. Postural representations have been characterized as having an external frame of reference – essentially a large category of potential representations that are primarily defined by being not somatotopic. There is evidence for processing tactile stimulus position in a variety of different external reference frames, including trunk-centered (Bartolomeo et al., 2004; Medina and Rapp, 2008), head-centered (Ho and Spence, 2007; Medina and Rapp, 2008), hand-centered (Liu et al., 2020; Moscovitch and Behrmann, 1994), and others. This suggests that the postural schema may involve several representations that are involved in representing the body in space, with future work needed to examine the nature of representations with these reference frames. Recent work has also provided evidence regarding the characteristics of postural representations with regards to multisensory integration. For example, Liu & Medina (2017) presented individuals with a variant of the mirror box illusion in which their hidden hand was in a different orientation compared to the mirror reflected hand (i.e., hidden hand palm up, mirror reflected hand palm down), and were asked to open and close the hands at the same time. Participants experienced a strong illusory rotation of their hidden hand such that they felt it matched the posture and movement direction of the hand in the mirror. Importantly, this illusion was modulated by the biomechanical constraints of the body, such that it was less likely for rotations that were more difficult to physically make, even though there was no actual physical rotation of the body in the task. These results suggest that postural representations include information not only about body position in external space, but information regarding the biomechanical constraints of the body as well (see also Parsons, 1987).

Body representations are not limited to our understanding of representing the location of touch. A variety of studies have expanded our understanding of other aspects of body representation, including tool use and body representations (Miller et al., 2018; Cardinali et al., 2009), peripersonal space (Serino et al., 2015; Makin et al., 2008), the persistence of body representations when limbs are missing (Flor et al., 1995; Ramachandran and Hirstein, 1998; Makin et al., 2015), conceptual and emotional representations about the body (e.g. somatorepresentation in Longo et al., 2010), embodiment (Longo et al., 2008; Tsakiris, 2010), and interhemispheric processing (Tamè et al., 2016). Taxonomic accounts of body representation have provided evidence for major divisions in body representations – in essence, carving cognition at its largest joints. Given the variety of phenomena involved in body representations, mechanistic explanations for how these representations develop, are generated, and maintained are unlikely to be captured by a taxonomic approach. Over the last twenty years there has been a large increase in strong empirical work on body representations. Combining these findings with processing models that go beyond taxonomic categorization will lead to a better understanding of body representations in future research.

## Related topics

Clinical disorders of body representations: A historical perspective; Predictive processing and body representation; Body models in humans and robots; Body representation in anorexia nervosa; Drug-induced alterations of bodily awareness

## Notes

1 Interestingly, although the term "superficial schema" has been used to describe this concept, it does not appear in Head & Holmes (1911). With regards to this representation, they write: "In the same way, recognition of the locality of the stimulated spot demands the reference to another 'schema.' For a patient may be able to name correctly, and indicate on a diagram or on another person's hand, the exact position of the spot touched or pricked, and yet be ignorant of the position in space of the limb upon which it lies. This is well shown in Hn. (Case 14), who never failed to localize the stimulated spot correctly, although he could not tell the position of his hand. This faculty of localization is evidently associated with the existence of another schema or model of the surface of our bodies which also can be destroyed by a cortical lesion. The patient then complains that he has no idea where he has been touched. He knows that a contact has occurred, but he cannot tell where it has taken place on the surface of the affected part."

2 My own work is not immune to this; see Liu and Medina, 2017 titled "Influence of the **body schema** on multisensory integration: Evidence from the mirror box illusion."

3 It is possible that tactile detection may not solely be mediated by primary somatosensory cortex. We (Medina and Rapp, 2008) reported an individual with an extensive lesion that removed nearly all of primary somatosensory cortex. Although this report focused on his phantom synchiric sensations, it is also interesting that he could detect tactile stimuli on his contralesional side – though note that his localization performance for these stimuli was severely impaired. Furthermore, non-human primates with removal of contralateral S1 and S2 can still detect touch (LaMotte and Mountcastle, 1979), and TMS to S1 does not impair detection thresholds (Tamè and Holmes, 2016). These results suggest a role for subcortical activity in conscious detection of touch.

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