On Proprioception in Action:

Multimodality versus Deafferentation*

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Abstract

Recent research on proprioception reveals that it relies on a systematically distorted model of bodily dimensions. This generates a puzzle about proprioception in action control: Action requires accurate bodily parameters. Proprioception is crucial for ordinary action, but if it relies on a systematically distorted body model, then proprioception should contain systematic errors. But we cannot respond by discarding proprioception from motor control, since we know from the severe problems deafferented agents face in acting that ordinary action requires proprioception. The solution is that the possibility of bodily action is provided for by multimodal body representations for action (the ‘body schema’).

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1. Introduction

Action is characteristically directed at external objects of interest; in acting, perception presents these objects and underwrites a sense of how well one is doing. Although one’s action ranges beyond the boundaries of one’s body, one is always acting with one’s body in some way. What are some conditions on bodily action? Intuitively, when we act to achieve our aims in the environment, we need to know – or at least compute over – the state of the effector (the thing one acts with) and what we have to do with the effector to achieve our aims. For example, if one wants to flick a switch, one has to bring one’s hand to where the switch is to flick it. How one does this depends on where the switch is and where one’s hand is, among other things. This suggests that if action is to be effective, we do not only need perception of the objects that we are acting on, such as the switch, but we also need some way of knowing the state of that which we are acting with, such as one’s hand.

This invites the question of what provides knowledge of limb position. Vision and other exteroceptive modalities certainly play a role in delivering the objects of action, the things we act on. What about the state of the effectors we act with? The primary effectors one acts with are one’s limbs. There is no doubt that vision and other forms of exteroception can provide information about the state of one’s effectors, since they can be objects of these perceptual modalities. We can see and touch our limbs. These perceptual modalities do not distinguish between objects which are parts of oneself and objects which are not. However, there are sense modalities dedicated to the registration of the state of one’s body and its parts. A case in point is proprioception. Proprioception provides a sense of the relative
position and movement of body segments from receptors in the joints and muscles. Through proprioception one can sense only the posture and movements of one’s own limbs, and no one else’s. As it is devoted to providing the spatial parameters characterising the current state of one’s limbs, proprioception appears to have a distinctive role in the control of bodily action.

But a closer look at proprioception reveals a striking difficulty. Recent research on proprioception reveals that it relies on a stored representation of bodily dimensions which is systematically distorted (Longo and Haggard 2010, 2012a, 2012b, Longo et al. 2012, Longo 2014). This generates a puzzle about the role of proprioception in action. On the one hand, action requires accurate bodily parameters to be successful; yet if proprioception relies on a systematically distorted model of bodily dimensions, then proprioceptive perception of limb position will be systematically inaccurate. This pushes us to jettison proprioception as a key source of parameters for motor control. Yet the case of deafferented agents, who have no proprioception and touch in large parts of their body, suggests the opposite. In the absence of proprioception, ordinary action as we know it is impossible: deafferented agents have severe problems in the online control of action. The conjunction of the problem raised by systematically distorted proprioception and the contrast between the character of afferented and deafferented action presents us with a challenge to articulate the distinctive role of proprioception in action: for action as we know it, we cannot do without proprioception, but it is unclear why.

In effect, consideration of the results from Longo and Haggard pushes us to separate these two questions:
1. What is the function of proprioception?

2. How does the motor system learn about limb position and movement for the control of action?

Intuitively, the function of proprioception is to provide the motor system with parameters about limb position and movement for the control of action. So answers to the two questions must coordinate. The central puzzle of this essay can then be described as follows. The systematic distortions in the implicit body model discovered by Longo and Haggard appear to drive a wedge between the two questions. Now the natural answer to the first question conflicts with the natural answer to the second question.

Grappling with the challenge teaches us three lessons: (1) The perception of one’s body required for acting with it is multimodal. This is because we can ameliorate the systematic distortions in bodily dimension present in proprioception only if body perception is multimodal. (2) In meeting the accuracy constraint required for action, we reveal that the conditions of possibility of bodily action are provided for by multimodal body representations for action (the so-called ‘body schema’). (3) Establishing the multimodal body schema as a condition of possibility of bodily action allows us to sharply restate our original question and, in so doing, focuses the central issue about the distinctive role of proprioception in action.

2. The Problem of Proprioception in Action
Proprioception provides us with the relative position and movement of body parts. However, the receptors it draws on provide information only about muscle stretch, tendon tension, and joint angles. How do we perceive limb posture and movement from afferent information about joint angles, tendon tension, and muscle stretch?

The question is particularly vivid in the case of joint angles. If receptors in joint capsules provide only joint angles between limb segments, without the length of the limb segments, it would be impossible to compute the location of limbs in space. Consider the position of one’s hand relative to one’s shoulder, for example. To compute this, we need to know the joint angles at the shoulder and elbow, and the lengths of the forearm and upper arm (see Figure 1). If we keep the shoulder and elbow joint angles and upper arm length constant, without information specifying the length of the forearm, the position of one’s hand would be simply indeterminate. It could be anywhere along the plane determined by the joint angles consistent with the degree of freedom of the elbow joint.

Figure 1. A body model specifying length of limb segments is required for proprioception (from Longo and Haggard 2010; reprinted with permission).
Without metric information about one’s body parts, proprioception would be unable to map input from its receptors to body part position in space. But no afferent signal carries this information. Thus, there needs to be a stored representation providing metric information about the body, which serves as a reference for proprioception and touch (Gurfinkel and Levick 1991, Longo, Azañón, and Haggard 2010). This representation is the *implicit body model*.

Accounts of proprioception have often assumed that this implicit body model carries accurate metric information about the body (Soechting 1982, van Beers et al. 1998, O’Shaughnessy 1980 and 1995). However, there is emerging evidence that the implicit body model is systematically distorted.

In a series of studies, Longo and Haggard investigated the implicit hand model underlying hand proprioception through a proprioceptive localisation task (Longo and Haggard 2010, 2012a, 2012b, Longo et al. 2012, Longo 2014). Their paradigm requires subjects to point to specific landmarks on their occluded stationary hand without touching it. Based on the localisation judgements subjects made in random order of the fingertips and knuckles on their left hand, Longo and Haggard could isolate the implicit hand model underlying proprioceptive localisation. Classical studies of proprioception have focused on determining the margin of error in proprioceptive localisation by comparing the judged and actual location of individual body parts. In contrast, Longo and Haggard were interested in determining the spatial relation between the landmarks localised, from which the structural configuration of the hand as represented in the implicit body model can be inferred.

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1 The implicit body model is required for mapping primary afference from tactile and proprioceptive receptors to stimulus or body part position in *external space*. It is a condition on tactile or proprioceptive perception in an *environmental frame of reference*.
For example, the length of a specific finger in the hand model can be determined by taking the distance between the localisation judgements of the fingertip and knuckle of that finger, irrespective of the localisation error specific to each judgement (see Figure 2). This structural approach allowed them to construct the size and shape of the hand as represented in the implicit hand model. The implicit hand model can then be compared to the actual hand.

![Diagram](image.png)

Figure 2. Isolating the hand model from location judgements of hand landmarks. Errors of location and rotation are ignored. Using the mathematical method of Procrustes superimposition, differences of location, scale, and rotation are removed so as to isolate the underlying morphology of the hand model (figures courtesy of Matthew Longo; reprinted with permission)

Longo and Haggard found a systematic distortion of hand size and shape. The implicit hand model represents the hand as broader and stumpier than the actual hand, with fingers shortened and knuckles wider apart (see Figure 3). Their basic result appears to be robust. It has been replicated in several studies on proprioceptive localisation conducted by various groups (Longo and Haggard 2010, 2012a, Lopez et al. 2012, Ferre et al. 2013, Longo 2014, Saulton et al. 2016), with different response measures (Longo and Haggard 2012b), in proprioceptive imagery (in as yet unpublished data from Longo’s lab), and even in a subject with a phantom
A Puzzle about the Function of Proprioception in Action

limb (Longo et al. 2012). Similar distortions of the implicit body model have also been found in touch using psychophysical methods, where subjects are asked to compare tactile stimuli of different lengths applied along and across the hand (Longo and Haggard 2011).

This is a striking result. It would appear that successful action requires knowing the state of the effector and what we have to do with the effector to achieve our goal. This would include knowledge of both the structure of the body, including the size and shape of body parts and their relative proportions, and its current posture. Whilst Longo and Haggard have only demonstrated distorted body models in the hand, there are grounds to think that the result may generalise to the rest of the body (see, e.g., Gurfinkel and Levick 1991). If proprioception depends on a distorted implicit body model, how can proprioception be providing the spatial parameters of bodily effectors for the control of action?

Figure 3. (Left) The actual hand. (Right) The hand model elicited by the localisation judgements shown as a deformation of the actual hand (from Longo and Haggard 2010; reprinted with permission).
I can now state the challenge that Longo and Haggard’s work issues for characterising the role of proprioception in action control. Proprioception must be accurate for bodily action. Proprioception relies on a systematically distorted body model, and thus is inaccurate. Yet bodily action is remarkably successful. Call this the Distortion Challenge. This is half of our puzzle about the function of proprioception in action. The other half comes from reflecting on deafferented agency.

One response to the Distortion Challenge would be to jettison the idea that proprioception is crucial to bodily action. However, we know that patients who have a near total loss of proprioception and touch suffer from severe problems in the online control of action (Cole and Paillard 1995, Rothwell et al. 1982). This suggests that proprioception is a crucial aspect of ordinary bodily action. Although studies of peripherally deafferented animals and humans have found that individuals retain the capacity for some purposive movement using peripherally deafferented limbs, these actions tend to be clumsier and lack the flexible adjustments characteristic of normal bodily action. Peripherally deafferented subjects also tend to have gross difficulties in learning new actions or adjusting established motor programs to unfamiliar circumstances.

There are significant individual differences in residual and restored motor abilities amongst peripherally deafferented patients. Generally some intact motor ability remains, though the extent of this differs. The few peripherally deafferented patients studied also differ in the degree of their sensory loss. Patient GL has no

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This assumption is taken for granted in the motor control literature (e.g. Ghez et al. 1990, Rossetti 1998). Assuming that proprioception must be (more or less) accurate for successful action, a further question concerns how fine-grained proprioceptive spatial information is. Researchers appear to assume that the spatial information provided by proprioception and vision is of comparable granularity (on internal models, see e.g. Kawato 1999, Ghez and Sainburg 1995; on visuo-proprioceptive conflict see e.g. Rossetti 1998, Ingram et al. 2000).
A Puzzle about the Function of Proprioception in Action

proprioception and touch up to her nose; patient IW is deafferented up to the collarbone level, but has intact neck proprioception (Cole and Paillard 1995). Patient GO has various somatosensory deficiencies in his arms and legs (Rothwell et al. 1982). GO and IW are able to walk, but GL cannot. GL and IW can perform many of the dexterous manual tasks that we take for granted in everyday life, but not GO.

The common factor in the recovery of motor control in these peripherally deafferented patients is their learning to employ constant visual attention in the control of action. In contrast to our effortless ability to act, deafferented agency requires constant visual vigilance (Cole and Paillard 1995, Ingram et al. 2000). The degree of visual attentional control needed for ordinary purposive activities for deafferented agents is overwhelming. Sneezing whilst walking, for example, disrupts IW’s concentration sufficiently to make him fall over.

Deafferented agency has little of the automaticity and ease characteristic of ordinary bodily activity (Cole 1991, Cole and Paillard 1995). This underlines the fact that bodily action for deafferented agents is different in kind from our bodily action. Given that the key difference between normal and deafferented agency is the presence or absence of proprioception, the difference in character of bodily striving between afferented and deafferented agency would appear to be due to proprioception (Wong 2015). Though the contrast, by itself, does not clarify what role proprioception plays, we may conclude that proprioception is crucial to ordinary bodily action.

The Distortion Challenge and the contrast between normal and deafferented bodily action pull us in opposing directions. The former suggests that proprioception is not necessary for ordinary bodily action, but the latter suggests that it is crucial.
A Puzzle about the Function of Proprioception in Action

Their conjunction generates the tension constituting the problem of this essay, which I am now in a position to pose.

The control of action appears to require proprioception, yet a distorted body model underlies proprioception. But if the implicit body model underlying proprioception were inaccurate, then proprioception itself would appear to be inaccurate. If proprioception were providing the parameters requisite for the control of action, action drawing on systematically inaccurate parameters would be ineffective. Yet action is remarkably successful; and, despite its inaccuracy, proprioception appears to be necessary, as the case of deafferented agents indicates. Call this the Problem of Proprioception in Action (or the Problem, for short).3

3. Responding to the Problem

There are three broad ways we can respond to the Problem of Proprioception in Action. (1) We can reject Longo and Haggard’s results, and, hence, deny that there is a Distortion Challenge. (2) We can reject the claim that the contrast between afferented and deafferented bodily action shows proprioception to be crucial. (3) We can try to answer how action is possible despite distorted implicit body models. My aim is to set aside the first two responses in favour of the third.

3 In expounding the Problem, I have moved between talking of the kind of information needed for action and what we need to know in order to act. This is deliberate, partly because formulations in terms of knowledge are more idiomatic. Deafferented agents lack proprioception altogether, conscious or non-conscious, so the distinction is immaterial for our Problem. Our Problem does not concern the explanatory role of consciousness in action (see, e.g., Eilan 2010 and Clark 2009). Our principal issue is that proprioceptive information does not seem to be suitable for guiding action.
A Puzzle about the Function of Proprioception in Action

The first response denies that there is a Distortion Challenge. Though we cannot rule out the possibility of alternative interpretations of Longo and Haggard’s data, the evidence for distorted implicit body models is strong. Their basic result has been replicated in numerous studies with different response measures. If their data merely derived from task-specific biases, we would not expect to see such a systematic distortion across these different studies in different conditions.

The second response denies that the contrast between afferented and deafferented bodily action shows that proprioception is crucial to ordinary bodily action. Given that peripherally deafferented agents lack both proprioception and touch, one way to develop this response is to distinguish between the contribution of touch and proprioception to ordinary bodily action. On this response, some of the specific character of deafferented agency may be traced to the tactile deficit of deafferented agents. Consider two examples from everyday agency. When placing one’s foot in walking, one relies on pressure sensors on the sole of one’s foot; these are lost. Also when gripping a cup, without the same tactile pressure sensors one doesn’t know how much force to exert.

Recognising that tactile loss in deafferented agents is responsible for some of the peculiar character of deafferented agency does not dissolve our Problem. First, we must note that both proprioception and touch will be affected by distortions in the implicit body model. This is because any somatosensory afference that needs to be mapped to a location in external space needs to be referred to the implicit body model. Second, observe that touch isn’t always operative, but proprioception is, because touch is a contact sense, but proprioception isn’t. Thus, we can compare instances of actions where there is no touch involved, such as reaching for
something (as opposed to grasping it). Furthermore, we can consider cases where we can factor out haptic exploration or feedback. So rather than looking at bipedal circumambulation, we should look at cases which don't involve standing. If we look at a case when deafferented agents are sitting or lying down and examine the character of their hand movements, say, in reaching toward an object or some part of their own body, it will be seen that this kind of action can be accomplished only with conscious attentional control for deafferented agents (Cole and Paillard 1995, Ingram et al. 2000).

Since each side of the conjunction that makes up the Problem of Proprioception in Action appears to be independently plausible, there is pressure to answer how action is possible despite distorted implicit body models.

But before I turn to developing an answer, let me make two remarks on the scope of the Problem. (1) The Problem applies to central instances of proprioception, conscious or unconscious. We are familiar from cases of blindsight and visual priming that perception without perceptual experience is possible. The same distinction can be made in the somatosensory realm. My concern is with the implicit body model underlying proprioception. It is plain that the systematic distortions of the body model affect proprioception regardless of whether the body model is engaged for conscious proprioception or for generating proprioceptive information which the agent is unaware of. This is because any primary afference from proprioceptive receptors – about joint angles, tendon tension, and muscle stretch – needs to be mapped onto an implicit body model containing body metric information for proprioception to provide a sense of limb position and movement in space.
It is true that Longo and Haggard’s proprioceptive localisation task requires subjects to provide a perceptual report of the location of fixed landmarks on their hand as they are consciously experienced – through pointing to them. The procedure is used to elicit the underlying implicit body model. So unless one thinks that the implicit body model may differ for conscious and unconscious proprioception, the issue does not arise. There are, as yet, no grounds for thinking that the implicit body model used to map primary afference differs depending on whether the upshot is proprioceptive experience or merely proprioceptive information. Thus it is plausibly the case that the functioning of proprioception requires an implicit body model whether we are concerned with conscious proprioceptive experiences or unconscious proprioceptive perception.

(2) The Problem afflicts central instances of bodily action and does not only pertain to certain exotic circumstances. It concerns normal bodily action. The Problem as posed does not rely on challenges arising from specific circumstances, for example (1) experimental scenarios involving conflict between visual and proprioceptive information, where subjects successfully act despite being under a proprioceptive illusion (e.g. Fourneret and Jeannerod 1998, Marcel 2003); or (2) the clinical and pathological cases. It remains open to an interlocutor to resist these cases by insisting that even though they reveal possibilities inherent in human agents, they do not reflect the situation of a normal agent acting with his body. We are not deafferented and we do not often face situations where visual and proprioceptive information conflict in everyday life. In contrast, the Problem of Proprioception in Action clearly concerns the condition of normal agents, since central instances of proprioception draw on the distorted implicit body model.
4. Multimodal Body Perception

How should we respond to the Problem? One route is suggested by a template matching experiment Longo and Haggard performed alongside the proprioceptive localisation task. Without seeing their hand, subjects were asked to pick out a visual image that best corresponded to their hand shape from an array of hand images which differed systematically with respect to their dimensions. Despite having a distorted hand model, subjects were accurate at picking out a visual image of their actual hand shape. Thus, subjects have an accurate conscious body image of their hand. This result suggests a dissociation between the implicit body model, as elicited by the proprioceptive localisation task, and the conscious body image, as indicated by the template matching task.

We can understand the body image to be a representation of one’s overall body form that can be manifest in consciousness through perception or imagery. In contrast with the implicit body model that is used to map primary afference from proprioceptive and tactile receptors, it is an explicit representation of body form, which may include the conscious awareness of current postural configuration. It is “given by the description or drawing or model one would assemble in order to say how the body seems to one at a certain instant” (O’Shaughnessy 1980: 241).

Clearly, vision is playing a role in giving subjects a sense of accurate hand shape, since subjects are able to pick out an accurate visual image of their hand shape without looking at their hand, even though proprioception does not deliver
A Puzzle about the Function of Proprioception in Action

this. Drawing on this line of thought, one response to this problem is that perception is multimodal: the senses do not work in isolation, and inaccuracies within one modality can be mitigated by collateral information about the same object from other sense modalities. Multisensory integration makes percepts more robust and accurate (Driver and Spence 2000, Ernst and Bülthoff 2004).

The suggestion is that body perception is multimodal. Even though there are perceptual channels dedicated to the registration of parameters concerning one’s own body and no other objects, these channels can be augmented by drawing on information from vision (Rossetti et al. 1995a, Graziano et al. 2000), and also motor information (effference copy) during movement (Fel’dman and Latash 1982). The key idea is that multisensory integration optimises information accuracy through drawing on a range of information sources. The range of information sources contributing will depend on the perceptual capacities of the agent. For example, vision will play a key role in the multimodal body perception for action in sighted individuals, but will play no role in congenitally blind agents (see section 5). In the blind, haptic perception and other sources play a more significant role in multimodal body perception (Lederman and Klatzky 2009, Jeka et al. 1996). Thus, with multimodality one’s overall body perception is more accurate.

Multisensory integration happens only when the perceptual system assumes that the sensory information it receives from multiple modalities is about the same event or object. This ‘unity assumption’ (Welch and Warren 1980) is key to multisensory integration in the case of body perception: the hand that one sees and

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4 Key recent discussions of the multimodality of body perception include Holmes and Spence 2006, Ehrsson 2012, and de Vignemont 2014. The thesis goes at least as far back as Schilder 1935.
feels is one and the same. A further thought is that the combination and integration of multiple sources of information helps to improve the accuracy of spatial parameters about one’s body. Ernst and Bülthoff (2004) distinguish two ways in which multiple sources of information about the same event or object are combined: sensory combination, where non-redundant sources of information are collected together, and sensory integration, where redundant signals are combined so as to reduce variance in the sensory estimate. In recognising that the senses do not work in isolation and that sensory combination and integration increase the robustness and accuracy of percepts, we begin to see how multimodal body perception can ensure that we have appropriately accurate spatial parameters that are needed for successful action.

My suggestion has been that the multimodality of body perception may provide a response to the Problem of Proprioception in Action. In what follows, I will examine two ways of developing this idea: multimodal body experiences and the multimodal body schema.

5. Multimodal Body Experiences

One way to develop the idea of multimodal body perception is to argue that conscious body experiences are multimodal (de Vignemont 2014).\(^5\) De Vignemont’s proposal is that conscious body experiences are multimodal because primary

\(^5\)Whilst the position developed in this section draws on strategies in de Vignemont (2014), she does not claim that multimodal bodily experiences guide action (see de Vignemont 2010).
A Puzzle about the Function of Proprioception in Action

somatosensory afference is mapped to a visual frame of reference in individuals who grow up with both sight and touch, but not in congenitally blind people.

Evidence for her claim comes from experiments on somatosensory temporal order judgements, where subjects are requested to judge the order in which their hands are touched without vision. If we compare the performance of subjects when their hands are crossed over the midline of the body (left hand on the right side of space, and vice versa), as opposed to when their hands are in an uncrossed position (left hand on the left side of space, etc.), we see a dramatic drop in performance. In the hands-crossed condition, subjects perform very poorly (Yamamoto and Kitazawa 2001a). We find this effect both in sighted and non-congenitally blind people, but not in congenitally blind people (Röder et al. 2004). This behavioural difference is best explained through a process of remapping stimulus information from a body part centred (somatotopic) frame of reference to a visual frame of reference that is absent in congenitally blind individuals. This finding indicates that the body representations underlying touch are different in kind in sighted (and late blind) people as opposed to congenitally blind people, since in their case it is centred on the body parts involved rather than on the visual frame of reference.

The thought, then, is that in the absence of the correcting presence of vision, proprioception would be inaccurate, but, in the normal case, vision is present to fix things. However, the response cannot simply consist in saying that vision is present, since there are two senses in which this might be the case. First, vision is ontogenetically present in the development of the kind of implicit body model that sighted individuals have. This is the sense drawn on to explain the remapping of touch from body centred to external frames of reference. But in this sense, the
A Puzzle about the Function of Proprioception in Action

implicit body model elicited by Longo and Haggard already bears the imprint of vision, since the subjects in their experiment were sighted individuals. So the observation that the ontogenetic presence of vision improves spatial parameters does not mitigate the inaccuracies that they discovered.

A second sense is that concurrent vision helps to improve the spatial accuracy of position sense. We need not think of position sense here as relying only on proprioceptive input, but also concurrent visual and motor inputs. However, does vision always help here? We know from experimental work on dissociations between sensory processing for perception and action that successful action is possible even when conscious perception is illusory, as is familiar from dissociations in the visual system (Milner and Goodale 2006; Jeannerod 1997). This point applies equally to conscious body experiences (Dijkerman and de Haan 2007). It has been shown that body representations for action can be systematically dissociated from body representations for perception, which underlie conscious proprioception. The former are comparatively unaffected by proprioceptive illusions (Lackner and Taublieb 1983, Marcel 2003, Kammers et al. 2006, Kammers et al. 2009a). In these cases we find that the spatial parameters determining conscious perception of hand location and the spatial parameters used in the control of action are distinct. Thus, even if de Vignemont’s line of thought shows that normal body perception is dependent on other sense modalities in addition to proprioception, it is far from clear that multimodal body experiences would provide an adequate answer to the Problem of

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6 My argument relies only on the possibility of dissociation between body representations for action and those for perception. Earlier experiments found that action was unaffected by proprioceptive illusions (Kammers et al. 2006 and 2009a), however, more recent evidence indicates that proprioceptive illusions affect at least some aspects of action under some conditions (Kammers et al. 2010, Newport et al. 2010, Zopf et al. 2011, Riemer et al. 2013).
Proprioception in Action. The dissociations between spatial parameters that figure in conscious perception as opposed to action control suggest that multimodal body experiences are the wrong place to pitch multimodality for solving a problem concerning the control of action.

6. The Multimodal Body Schema

I suggest that we should think of multimodality as coming in at the level of the body representations for action: the body schema.

Haggard and Wolpert characterise the body schema as follows:

*Body schema* refers to a representation of the positions of body parts in space, which is updated during body movement. This typically does not enter into awareness, and is primarily used for spatial organization of action. The body schema is therefore a central representation of the body’s spatial properties that includes the length of limb segments, their hierarchical arrangement, the configuration of the segments in space and the shape of the body surface. (Haggard and Wolpert 2005: 261).

The key thought is that the body schema is a dynamic representation of the relative position of body parts that is employed in the control of action and the maintenance of posture. Since the body schema is crucial for online control of action, it has to be constantly updated with bodily movement as the action unfolds (Wolpert et al. 1998,
Schwoebel and Coslett 2005). Because of constraints on accuracy, it is plausible to think that body representations for action will draw on a range of different sources, including vision, touch, proprioception, the vestibular system, and the motor system, so as to provide the most optimal information for the control of action. This will involve both sensory combination and sensory integration from multiple sources of information about bodily parameters required for action (Ernst and Bülthoff 2004). On this picture, there are architectural and computational grounds for thinking that the body schema must be multimodal.

The suggestion here is that the multimodal body schema is what allows us to answer the Distortion Challenge. What we are doing is rejecting the first premise of the Distortion Challenge, that proprioception must be accurate for bodily action. Rather there are multimodal body representations which provide the most optimal information about limb position and movement for the control of action. The use of multiple, collateral sources of information to compute the spatial parameters of bodily effectors provides the optimal estimate of limb position and movement, and neutralises the systematic distortions of the implicit body model. Thus the very possibility of bodily action is underwritten by the multimodal body schema.

But there is scepticism about the notion of ‘body schema’. In order to earn the right to use body schemata as an explanatory notion, I need to answer these sceptical doubts. The key worry is that the notion fails to be explanatory because it is not well defined. Expressing this concern, Maravita, Spence and Driver write: “the ‘body schema’ has often been invoked as an explanatory concept, when it should perhaps rather be considered as a label for a set of problems still requiring explanation” (2003: 531).
I will reply by providing a functional characterisation of the body schema and then providing some arguments for it. My strategy is to argue that there must be some body representation that fulfils a certain role and to understand the body schema as that which does this. I will provide two arguments for the body schema: (1) from reflection on Bernstein’s degrees of freedom problem in motor control and (2) from perception/action dissociations. Following that, I will argue from observations about tool use that the body schema is multimodal.

Bernstein’s (1967) degrees of freedom problem is that if the information processing system were involved in the production of all decisions about each of the muscles involved in a motor act, this would be computationally much too expensive. Why? The motor system has too many degrees of freedom. For even simple movements, there are numerous joints and muscles involved. This would lead to an impossible situation for the central nervous system if it had to control all these degrees of freedom separately (Bernstein 1967, Greene 1972, Whiting 1984).

What Bernstein shows is that there are too many parameters to control individually. These control parameters need to be organised hierarchically, so as to reduce degrees of freedom. On a hierarchical model of action, actions are organised in a tree-like structure, with the overarching goal of the action at the top of the hierarchy, followed by sub-goals under, and different levels of the hierarchy, eventually terminating in individual muscle activations. The idea is that if certain action units are grouped together and hierarchically controlled, control of nodes higher up the hierarchy programs the operation of nodes lower in the hierarchy. For example, plans allow the agent to orient his behaviour in some general way, and a descending hierarchy of systems implement these plans ever more specifically as we
work down the control hierarchy. A consequence is that the operation of various action units lower down the hierarchy will be automatic. Though the agent does not monitor the operation of these units, the successful operation of these action units still requires that the motor system possesses accurate information about the relevant bodily parameters. Without having a body schema this would not be possible.

The imposition of the motor hierarchy requires both automaticity and the body schema, and it is the coming together of the two that shows how control of a complex motor system with numerous degrees of freedom, in real time and with limited computational resources, is possible. There is a deep link between automaticity and the body schema that deserves further exploration. But I have said enough to show that the current position of body parts relative to other body parts has to be registered in order to make motor control in real time possible.

As noted earlier, we know from experimental work on dissociations between perception and action that successful action is possible even when conscious perception is illusory. Together with the degrees of freedom problem, this suggests that there must be some representations employed for action which are automated and which are accurate. We can identify these as the appropriate body representations for action which play the functional role which we have identified for the body schema: the provision of accurate parameters for the control of action. Thus there are grounds for thinking that the architecture of motor control requires a hierarchical model of action where there are automated parameters figuring in representations for action control. These same representations are isolated when we encounter successful action under conditions of illusory perception.
We now have architectural grounds for positing the body schema for action. But the question arises as to why the body schema should be thought to be multimodal. If we consider the domain of tool use and its consequences for action, then there is strong evidence for multimodality, as tool use requires rapid integration of the tools into one’s body schema for action.

When Head and Holmes introduced the notion of ‘body schema’ in 1911 they explicitly noted the importance of the notion of a body schema where tools could be incorporated into motor representations:

It is to the existence of these “schemata” that we owe the power of projecting our recognition of posture, movement and locality beyond the limits of our own bodies to the end of some instrument held in the hand. Without them we could not probe with a stick, nor use a spoon unless our eyes were fixed upon the plate. Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of these schemata... (Head and Holmes 1911: 188).

Evidence that tool use requires the body schema to be multimodal comes from two directions. We can examine the effects of tool use on perception and on action. On the perceptual side, it has been shown in monkeys that when they learn to use a tool, there is an extension of the bimodal receptive fields to the reaching area of the tool (Iriki et al. 1996, Maravita and Iriki 2004). The peripersonal space around the hand expands to cover the extent of the tool. Furthermore, there is behavioural evidence from performance on temporal order judgment tasks that the
somatosensory system treats tools like arm extensions. Earlier we saw the difference in performance on temporal order judgements made by congenitally blind versus late blind and sighted people when their hands are crossed over the midline. Similar effects are observed with tool use. If a subject’s hands are uncrossed, but tools held in his hands are crossed over his midline, then performance in temporal order judgement tasks in sighted individuals drops, like in the hands-cROSed condition without tools. There is a similar drop in performance if the subject’s hands are crossed but the tools are uncrossed. Interestingly, if the subject’s hands are crossed, but the tools are also crossed so that the tips of the tools would be roughly where they would be if neither hands nor tools were crossed, then task performance goes back to the same level as the hands-uncrossed condition (Yamamoto and Kitazawa 2001b).

These studies support the idea that tools are perceptually treated as body extensions, as Head and Holmes (1911) anticipated. The updating of one’s body schema when tool extensions are involved is naturally construed multimodally. We do not have proprioception in tools. The expanded receptive fields in Iriki’s monkey studies were of bimodal neurons sensitive to visual and tactile input. The recovery in performance in the condition when both hands and tools are crossed to levels in the hands-uncrossed condition indicates that the processing of tools as part of one’s body in external space is anchored to visual frames of reference rather than to a somatotopic one. These results provide perceptual evidence for body schema extensions with tools. Is there evidence from action that tools are treated as part of one’s body?
A recent study by Cardinali and colleagues (2010) provides evidence that the kinematic profile of reaching and grabbing with a tool is just like that of having a lengthened limb. Jeannerod (1999) analysed the kinematics of reaching and grasping hand movements, and showed that these could be divided into a transport and a grip component. Cardinali and colleagues asked subjects to perform pointing and grasping tasks with and without a 40 cm long mechanical grabber. Subjects first performed free hand movements, followed by grasping movements with the grabber, and then the same free hand movements as before. They found that the kinematic profile of the free hand pointing and grasping movements made after tool use showed differences in the transport component that are best explained by a modification of the somatosensory representation of the subject’s arm. The arm is represented as being longer than it is, which is a residual effect of tool use. This was corroborated by evidence from comparing stimulus localisation judgements through blindfolded pointing on landmarks on the hand before and after tool use. The modification of the body schema through tool use in these cases is clearly multisensory. Visual, somatosensory, and motor information is feeding into the updated representations of limb length for online control.

I have argued that there are architectural reasons why there should be something like a body schema, so as to solve the degrees of freedom problem. There is evidence that such a schema explains action control under conditions of illusory body perception. Furthermore, such a schema can incorporate foreign objects into one’s body, such as tools, if these function like limb effectors. The need for plasticity in the body schema as that which underlies action control means that such a schema must be able to incorporate tools. This requires the body schema to be multimodal.
The multimodal character of the body schema is what neutralises the systematic distortions present in the implicit body model. Thus, the multimodality of body representations in action – the body schema – is what answers the Distortion Challenge.\footnote{I have not attempted to explore why we have such distorted implicit models. This is not to deny that these distortions could be adaptive. I take my argument to show that these distortions must be dealt with through multisensory integration in some way, though I have left the specifics of how the ‘neutralisation’ proceeds open. For possible ways, see, e.g., Ernst 2006, Alais et al. 2010; for discussions of how different sources of sensory information are weighted in multisensory body perception, see Shenton et al. 2004 and Kammers et al. 2009b.}

7. Revisiting the Original Problem

How does the multimodal body schema bear on the Problem of Proprioception in Action? Our problem is that proprioception appears to be inaccurate but yet, in some way, obligatory for action. The multimodal body schema provides for the conditions of possibility for bodily action. But now that we have the multimodal body schema in view it exacerbates our original problem. Though Longo and Haggard have provided powerful evidence that we have distorted body models, reflection on the case of deafferented agents and their altered mode of action control suggests that proprioception has some special role, which remains to be articulated.

If proprioception were just one source among several providing information about bodily effectors, then it would fail to explain why the loss of proprioception is so debilitating for deafferented agents. One way to see this is to consider whether the body schema is compromised in deafferented agents. It has been argued that the body schema is missing in deafferented patients, based on arguing that the
contrast between peripherally deafferented patients and numbsense patients presents a double dissociation between the body image and the body schema (Cole and Paillard 1995, Paillard 1999).

Paillard argues for this double dissociation as follows. In numbsense, the somatosensory analogue of blindsight, patients suffer from a central deafferentation of a limb and are unaware of tactile and proprioceptive stimulation on the affected limb (Paillard et al. 1983, Rossetti et al. 1995b, 2001). When tactile or proprioceptive stimuli are applied in the absence of vision, numbsense patients are at chance when verbally reporting the site of stimulation or when pointing on a diagram of the affected limb, but they are able to reliably point to the site of stimulation (or its position) on the affected limb with the unaffected hand. In contrast, if nociceptive or thermal stimuli are applied to peripherally deafferented patients in the absence of vision, they are able to identify the site of stimulation through verbal report or pointing on a picture of the body. (Though these patients have lost touch and proprioception, pain and temperature sensation are intact as the afferent nerves underpinning these functions are unaffected.) However, they are unable to point to the site of stimulation in the absence of vision. Thus Paillard claims that the body schema is intact in numbsense patients – because they can point to the site of stimulation without vision – and absent in peripherally deafferented patients – because they cannot point to the site of stimulation without vision. The situation is the reverse with the body image, which is intact in peripheral deafferentation but absent in numbsense.

There is no question that there are significant differences between the two pathologies. But it is unclear that the two cases are appropriately complementary in
A Puzzle about the Function of Proprioception in Action

A way that supports a double dissociation. The key point is that Paillard thinks that the body schema is absent in peripherally deafferented patients because they cannot point accurately in the absence of vision. We can agree that there is an absence of proprioceptive input in the case of peripherally deafferented agents, and that this explains why they cannot point accurately in the absence of vision. But why does this entail that the body schema is absent?

Paillard’s use of the inability to point in the absence of vision as criteria for the loss of the body schema assumes that proprioception is necessary for calibrating the body schema. This assumption is widespread (Cardinali et al. 2009, Paillard 1999, 1982, Cole and Paillard 1995, Gallagher and Cole 1995). But it is unwarranted.

What follows from this deficit is only that the body schema is typically calibrated by proprioception, and that, in the absence of proprioception or any substitute information channel, its operation is defective. The natural response is that the body schema is compromised by peripheral deafferentation, as a key source, or the key source of input, is now missing. As I have argued, the body schema consists of those body representations underlying action. Thus, insofar as deafferented agents can act, they must have some intact body schema, though these will be lacking inputs from proprioception, but will rely heavily on vision. In relearning how to act after peripheral deafferentation, these agents are recalibrating their body schema to operate with vision.

The functional conception of the body schema I have advocated allows me to both reject the claim that intact proprioception is necessary for possession of a body schema, whilst recognising that proprioception is critical for calibrating the body

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8 Compare de Vignemont 2010: 675.
schema so that bodily action has the character it ordinarily has. In striving with one’s body, one is not like a pilot in a ship (Brewer 1993); normally, one does not have to observe one’s body in striving with it so as to control one’s action. Thus, it can be seen that the capacity for proprioception is vital to ordinary bodily action.

This sharpens my original question: what about the lack of proprioceptive input to the body schema explains why the character of deafferented action is different from ordinary bodily action? There are other sources of information which deafferented agents can draw on which do not suffer from the systematic distortions present in proprioception, such as vision and motor information. What about proprioception is special here? Why is its absence so grave? It is inaccurate, but yet is obligatory for ordinary bodily action. Is it simply because of differences between the pervasiveness of proprioception and vision? Proprioception is always operative and provides a constant source of information whether one is paying attention to it, whereas vision requires that one’s eyes are open and oriented toward the seen object – yet one is not always looking at one’s body whilst acting.

This quantitative aspect does not appear to be the crux. One way to bring out the sense in which proprioception is a special source of information is to contrast the effects of the loss of vision as opposed to proprioception. Blind agents are able to act with their bodies just like sighted agents, even though they make more errors compared to sighted agents, because there is less information available. However, the loss of vision does not result in a change in the character of bodily striving. Blind agents do not have to constantly consciously control their basic actions the way
A Puzzle about the Function of Proprioception in Action

deafferented agents have to. Blind agents may have to pay more attention to locate external objects which they act on; they may have to probe around to find the target object of their actions (with their cane, for example), but the probing itself is done with a limb which they control effortlessly. In contrast, deafferented agents have to consciously control their basic actions even if they can see the objects that their actions are directed at. Even though blind agents cannot see, in striving with their bodies, they are not in their bodies like pilots in ships, unlike deafferented agents.

In this way, we can see that proprioceptive loss is not simply a loss of one information source about one’s body among others. Proprioception is a source that shapes the very character of ordinary bodily action. It is only when we gain an appreciation of proprioception as a distinctive source of spatial information about one’s bodily effectors that we grasp the profundity of the Problem of Proprioception in Action.

8. Conclusion

Our problem is that proprioception appears to be inaccurate but yet, in some way, obligatory for action. Through reflecting on the conditions of possibility of bodily

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9 This contrast only requires an intuitive notion of basic action. An example is thrusting one’s hand out for a handshake, or tying one’s shoelaces when one has acquired the skill of doing so. The relevant notion is that of teleologically basic action (Hornsby 1980): roughly, those actions the performance of which does not require procedural knowledge of how to perform another action.

10 The contrast here has its basis in phenomenology, but is assumed in research on spatial perception (especially active touch), spatial action and locomotion of blind individuals (Révész 1950, Strelow 1985, Klatzky and Lederman 2002). This can also be brought out by how the blind do not in general have problems walking, but the deafferented do. Even in cases when deafferented agents regain the ability to walk, it requires a long period of relearning and exploits new motor control strategies (Cole 1991).
agency and the role of multimodal body perception in action, I have sharpened our question about the role of proprioception in action and our appreciation of proprioception as a special source of information about ourselves. My proposal – that proprioception feeds into the construction and maintenance of a multimodal body schema – suggests one way in which proprioception could figure in action control.

I have argued that the accuracy constraint on successful bodily action sets demands on the representations that can underlie action control. Accuracy is achieved through multisensory integration reducing errors in multimodal body representations in action. We saw that the need for the body schema arises from architectural grounds from a motor hierarchy in action control and requirements for body extensions through tool use. The presence of such a representation was revealed in perception/action dissociations. Thus we see that the conditions of possibility of bodily action are provided for by multimodal body representations for action (the body schema). This is one side of the coin. The claims that the body schema is what underlies the possibility of action and that proprioception is crucial for ordinary bodily action do not yet tell us what is missing in the case of deafferented agents. The facts suggest that the proper operation of the body schema depends on intact proprioception. But a positive account of the distinctive role of proprioception remains to be articulated.\textsuperscript{11}

\textit{Philosophisches Seminar}

\textsuperscript{11} I present an account of how the capacity for proprioception is a condition on the capacity for afferented bodily agency in Wong 2017.
A Puzzle about the Function of Proprioception in Action

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A Puzzle about the Function of Proprioception in Action

References


A Puzzle about the Function of Proprioception in Action


A Puzzle about the Function of Proprioception in Action


A Puzzle about the Function of Proprioception in Action


A Puzzle about the Function of Proprioception in Action


A Puzzle about the Function of Proprioception in Action


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A Puzzle about the Function of Proprioception in Action


