Distorted body representations and skilled action

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Abstract

Several aspects of somatosensory perception require that immediate sensory signals be integrated with stored representations of body size and shape. Recent research has revealed that both tactile size perception and position sense rely on highly distorted representations of the body. The presence of such distortions raises a fundamental problem. The lack of proprioceptive afferent information is known to cause devastating impairments in skilled action, suggesting that position sense plays a critical role in skilled action. How then can the obvious fact of skilled action co-exist with distorted representations of the body? In this chapter I will review research on distorted body representations underlying position sense and discuss several ways in which such distortions might be reconciled with dexterous action. I will end with some speculations about the implications of such distortions for our sensation of movement.

Action necessarily involves a change in the location of body parts, and awareness of action is in large part an awareness of this change. Perceiving the location of body parts in external space requires that immediate sensory signals be combined with stored representations of body size and shape. Recent studies have found that these representations are highly distorted, at least in the specific case of the hand. This raises the question how skilled action can co-exist with distorted body representations underlying position sense. In this chapter I will discuss research investigating body representations underlying position sense and describe several ways in which the existence of such distortions might be reconciled with the clear fact of dexterous action. I will finish with a brief discussion of the implications of this research for motor awareness.

Distorted body representations underlying position sense

Several classes of sensory signals provide information used for position sense. Receptors in joints themselves signal flexion or extension, receptors in the skin signal the extent to which the skin is stretched, and receptors is muscle spindles signal muscular contraction or lengthening (for review see Proske & Gandevia, 2012). These signals, along with efferent copies of motor commands provide information about the overall postural configuration of the body (Burgess, Wei, Clark, & Simon, 1982). It is critical to note, however, that all of these signals provide information about the *angles* of the different joints, that is the relative degree of flexion or extension at each joint. No signal – or combination of signals – provides direct information about the absolute location of body parts in external space.

The location of body parts is, thus, not specified by anything resembling a global positioning system (GPS) signal, but rather must rely on something more analogous to

"dead reckoning", in which the location of a body part is specified by the combination of the direction each joint is oriented with information about the distance between each adjacent pair of joints. This situation is depicted in the left panel of Figure 1. To perceive the location of a distal body part such as the wrist relative to the shoulder, information about the angles of the shoulder and elbow joints ($\theta_{shoulder}$ and θ_{elbow}) needs to be integrated with information about the lengths of the upper arm and forearm ($Length_{upperarm}$ and $Length_{forearm}$) connecting the joints together. While the angles are specified by immediate sensory signals, the lengths are not, and thus must come from stored representations of body size and shape. It is, of course, not mysterious where such representations might come from, given the constant presence of the body in our visual field and our lifetime of experience with it. The point is simply that position sense requires that immediate sensory signals be integrated with stored representations of body size and shape, what Longo, Azañón, and Haggard (2010) called a *body model*.

Figure 1: *Left panel*: Schematic illustration of the need for a body model in position sense. Perceiving the position of the wrist relative to the shoulder requires information not only about joint angles ($\theta_{shoulder}$ and θ_{elbow}) but also about the length of the upper and forearm ($Length_{upperarm}$ and $Length_{forearm}$). While information about joint angles is specified by immediate proprioceptive signals, information about body part length is not, suggesting it must come from a stored body model. *Centre and right panels*: The paradigm of Longo and Haggard (2010) for measuring the body model. The participant lays their hand flat on the table (centre) and uses a long baton to indicate the perceived location of landmarks on their hand on an occluding board (right). Responses are captured by an overhead camera. The size and shape of the body model can be assessed by investigating the internal configuration of localizations of multiple landmarks, without regard to differences in actual and perceived location

The need for something like a body model for position sense has been identified by numerous researchers over the past several decades (e.g., Craske, Kenny, & Keith,

1984; Gurfinkel & Levick, 1991; Soechting, 1982; van Beers, Sittig, & Denier van der Gon, 1998), but it has generally been assumed that such information is readily available and unproblematic. This assumption seems reasonable for several reasons. First, while the size and proportions of the body may change over developmental time scales, on a day-to-day basis the body is largely constant. Second, the body is ubiquitous in perceptual experience, and indeed is probably the most familiar object we perceive. Finally, as discussed in more detail below, lack of accurate information about the body would seem to pose fundamental problems for skilled action. Nevertheless, Gurfinkel and Levick (1991) reported intriguing anecdotal evidence suggesting that position sense may, nevertheless rely on a distorted body model. They asked participants to localize two parts of their arm in external space, finding that the distance between the judged locations was less than the true distance between those parts.

Longo and Haggard (2010) developed a task to measure the body model underlying position sense in the case of the hand. The participant places their hand palm-down on a table underneath an occluding board. The participant is then asked to localize different parts of their hand by placing the tip of a long baton on the place on the board directly above where it feels like each part is located. This paradigm is shown in the right two panels of Figure 1. Across trials, participants localized 10 landmarks, the tip and the knuckle of each finger. Previous studies of position sense have generally focused on the so-called 'error of localisation', the different between the true location of a landmark and the participant's judgment. By obtaining localization judgments for multiple landmarks, however, this paradigm takes a fundamentally different approach and investigates the *internal configuration* of judged locations for the different landmarks, completely ignoring the relation between actual and judged location. This

allowed Longo and Haggard (2010) to construct perceptual maps of the representation of hand size and shape.

The resulting perceptual maps from 18 participants in Experiment 1 from Longo and Haggard (2010) is shown in Figure 2. The perceptual maps (in black) from each participant were placed in mutual alignment using a statistical method called Procrustes alignment (Rholf & Slice, 1990), which superimposes each map, removing differences in location, rotation, and size. This allows a grand-average perceptual map to be constructed, as depicted by the black lines. For comparison, an analogous map was constructed for the actual configuration of participants' hands, depicted by the grey lines. Remarkably, the perceptual maps were highly distorted, and in a consistent manner from person to person. Specifically, there were three clear patterns of distortion: (1) overestimation of hand width (i.e., the distance between pairs of knuckles); (2) underestimation of finger length (i.e., the distance between the knuckle and tip of each finger); and (3) a radial-ulnar gradient, with underestimation of finger length increasing from the thumb to the little finger.

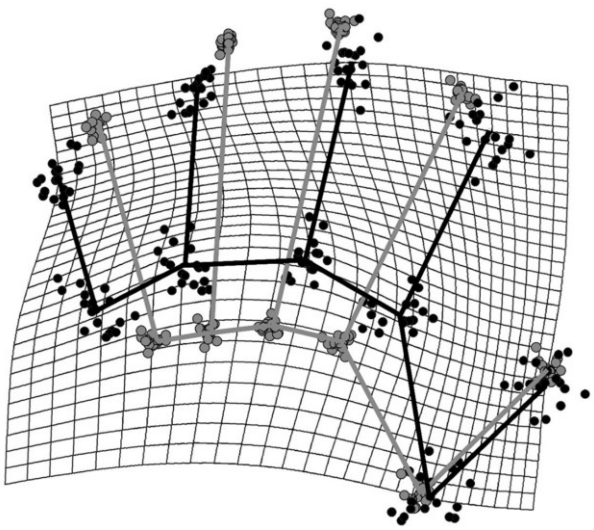

Figure 2: Perceptual maps from the study of Longo and Haggard (2010, Experiment 1). The grey dots represent the actual locations of the tips and knuckles of the fingers of the left hands of 18 participants. These maps were aligned using Procrustes superimposition, which translates, scales, and rotates maps

into best-fitting alignment. The black dots show the judged locations of each landmark. Again, maps from different participants were placed into best-fitting Procrustes alignment. The warped grid shows how a perfectly square grid superimposed onto actual hand shape would have to be deformed to transform actual hand shape into represented hand shape, using a thin-plate spline.

These distortions bear intriguing similarities to known distortions of the somatosensory system. For example, the overestimation of hand width compared to length mirrors anisotropies found in the geometry of the receptive fields of individual neurons in the spinal cord and primary somatosensory cortex which are generally shaped like ovals elongated along the proximo-distal limb axis (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961; Brown, Fuchs, & Tapper, 1975). Similarly, the perceived distance between two touches is bigger when the touches are oriented across the width of the hand than along it's length (Green, 1982; Longo & Haggard, 2011; Le Cornu Knight, Longo, & Bremner, 2014; Miller, Longo, & Saygin, 2014). On the glabrous skin of the palm, receptive fields of somatosensory neurons tend to be more circular than on the hand dorsum (DiCarlo & Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). Correspondingly, there is also a reduction in the anisotropy of perceived tactile distance on the palm (Longo & Haggard, 2011; Longo, Ghosh, & Yahya, 2015a) and in the distortions of perceptual maps of position sense (Longo & Haggard, 2012a). Thus, there appears to be a mutual inter-relation between the geometry of receptive fields in somatosensory cortex, the perceived metric properties of touch, and the body model underlying position sense.

Subsequent studies have replicated this basic pattern of distortion in the body model under a wide variety of conditions (Ferrè, Vagnoni, & Haggard, 2013; Longo, 2014, 2015b; Longo & Haggard 2012a, 2012b; Longo, Long, & Haggard, 2012; Longo, Mancini, & Haggard, 2015b; Lopez, Schreyer, Preuss, & Mast, 2012; Mattioni & Longo, 2014; Mattioni, Ganea, & Longo, 2015c; Saulton, et al., 2015, 2016). For example, clear

distortions are found for both the right and left hands (Longo & Haggard, 2010), with the hand in various postures (Longo, 2015; Longo & Haggard, 2012), with the presence or absence of visual input (Longo, 2014), when participants localize touch rather than verbally-specified landmarks (Longo et al., 2015b; Mattioni & Longo, 2014), and even to an extent for non-hand objects (Saulton et al., 2015). Two recent studies, however, have found that the magnitude of distortions is clearly reduced when participants localize landmarks on a seen rubber hand based on visual memory (Longo et al., 2015c; Saulton et al., 2016).

Longo and Haggard (2010) argued that this distorted body model underlying position sense is distinct from the conscious body image. In addition to the localization task described above, they obtained measures of the body image of the hand using a 'template matching' procedure (Gandevia & Phegan, 1999). Participants were shown an array of images of left hands that had been stretched to have different shapes, some being very long and slender, and others highly squat and fat. They chose from the set of images the one most similar in shape to the perceived shape of their own left hand. No sign of distortions like those found with the localization task was apparent for the body image, however, a result consistent with several subsequent studies (e.g., Longo, 2015c; Longo & Haggard, 2012b). On the basis of this dissociation, Longo and Haggard (2010) claimed that position sense relies on an implicit representation of the body, which while massively distorted remains inaccessible to conscious introspection. Subsequent research has suggested that some types of body image judgments may show some evidence of similar distortions (Longo & Haggard, 2012b), and aspects of the distortions such as the overall underestimation of finger length may reflect conceptual misunderstanding of where the knuckles are located in the hand (Longo, 2015d; Longo et al., 2015c; Margolis & Longo, 2015).

How can distorted body representations coexist with skilled action?

The results presented in the previous section provide clear evidence the position sense relies on a massively distorted representation of body size and shape, at least in the case of the hand. This begs the question of how our obvious ability to act dexterously can co-exist with such distortions. A first approach to this question might suggest that proprioception simply isn't of critical importance for action. This view, however, is dramatically contradicted by cases in which people have lost proprioception, which results in massive impairments in skilled action (Cole & Paillard, 1995; Rothwell et al., 1982). For example, consider the case of patient I.W., described vividly by the neurologist Jonathan Cole (1995) in his book *Pride and a Daily Marathon*. At the age of 19, I.W. suffered a near total loss of sensory fibers below the neck following an auto-immune reaction, leaving him with a complete loss of tactile and proprioceptive signals from the body. Critically, however, efferent signals carrying motor information to the body were not affected. If position sense (and touch) were not critical for skilled action, then I.W. should have had only modest, if any, motor difficulties. In fact, I.W. was profoundly impaired in his ability to act. In the immediate period following his deafferentation, I.W. was unable to sit up, stand, walk, pick up or hold object manually, or even to feed himself. Over a period of years, I.W. taught himself how to control his actions, learning again to walk, to perform household activities, and even to drive a car, a story movingly told by Cole (1995).

From the current perspective, however, the critical point is that I.W. learned how to perform these actions in an entirely different way than neurologically intact people. Actions which are effortless to most people, such as walking, require intense concentration and constant visual attention for I.W. He has learned to compensate for

the loss of position sense, but his story nevertheless dramatically emphasizes the critical role of proprioception in everyday skilled action. Thus, position sense appears to be critical for skilled action and also to rely on a highly distorted representation of the size and shape of the body. This seems to raise a dilemma about how dexterous and skilled action can exist alongside large distortions, a problem that Wong (in press) has called 'the distortion challenge'. In the remainder of this section, I will discuss four ways in which the distortion challenge might be answered.

First, one might question whether systematic, constant errors are any more problematic than random, variable errors. The distortions described above might lead to consistent errors of movement being made in the same direction across multiple attempts. It is well established, however, quite aside from the issue of distortions that passive position sense is highly inaccurate, with large trial-to-trial variability. For example, Tillery, Flanders, and Soechting (1991) asked participants to use a pointer to judge the perceived location of their hand following a passive movement. Not only were participants poor at performing this task, but they were highly inconsistent from trial-to-trial. In terms of the consequences for motor control, it is not obvious why systematic distortions, which would lead to constant errors, are any more problematic than purely random variable errors. It is no more problematic to mis-reach consistently to the right than to miss by an equal amount, but in a random direction on each trial. Indeed, constant errors could be thought of as less problematic because they can be learned and correctly with practice, unlike random variable errors. From this perspective, the problem for skilled action is not distortion per se, but error more generally. This argument does not, of course, provide any insight into this problem, but simply suggests that the presence of the distortions described above does not provide any additional problem over and above the variable error which is well known from previous research.

Second, the distortions described above concern only the use of position sense to perceive the absolute location in space of part of the body. According to the logic of Longo and Haggard (2010) described above only joint angles are specified by immediate afferent signals, and a body model is required for using this information to identify exactly where part of the body is located. But for many uses of proprioception in motor control information about joint angles may be sufficient. Consider, for example, the adjustments we make to the distribution of our weight onto our feet as we stand or walk. One important function of such adjustments is to ensure that weight is not distributed in such a way that our ankle rolls, which could result in a sprain or break. For this purpose, knowing the absolute location of the ankle in external space is irrelevant. What matters instead is that the ankle remain within a safe range of rotation. The rapid adjustments we make if we accidently step on the edge of a curb show the sensitivity of the motor system to the rotation of the ankle joint. For this purpose, a body model is not needed and the distortions described above are irrelevant. It is likely that many other uses of proprioception in skilled action similarly depend largely or exclusively on monitoring of joint angles, rather than absolute spatial locations.

Third, some studies have suggested that limb movements may be specified in terms of the relative tension of agonist and antagonist muscles required to achieve the desired final position, a model known as 'final position control' (e.g., Bizzi, Accornero, Chapple, & Hogan, 1984; Polit & Bizzi, 1978). This contrasts with the model of motor control in which a movement is coded as a vector deviation from a perceived starting position to a desired ending position. The important point about final position control in the present context is that it does not require that the absolute starting position of the limb be known. Consider, for example, the experiment of Polit and Bizzi (1978). Monkeys were deafferented so that, like patient I.W., they had no proprioceptive ability

to perceive the location of their arms outside of vision, and trained to reach for a light. Sometimes the lights in the room would be turned off before the monkey reached, so that they were dependent on their memory of the visually-specified location of their arm. The critical condition was the case in which the monkey's arm was displaced after the lights had gone off, but before the monkey had started their reach. As the monkey had no way of knowing that it's arm had moved, movements coded as a vector deviation from the starting location should have resulted in systematic misreaching by an amount equal to the unseen displacement. In contrast to this prediction, the monkeys were able to reach successfully for the light. Thus, despite being completely unaware of the starting location of the limb, the monkey was nevertheless able to place the limb in the desired final state. This suggests that the movement had not been coded in terms of its absolute spatial trajectory, but rather in terms of the relative degrees of flexion and extension of the pairs of antagonistic muscles controlling limb posture. Thus, to the extent that skilled action relies on specification of endpoints and does not require detailed specification of starting locations, then distortions of position sense may pose relatively modest problems for behaviour. The misperceptions of limb perception due to the distortions described above are relatively small compared with the misperceptions of the monkeys in Polit and Bizzi's (1978) study, which nevertheless did not impair their ability to successfully reach for desired targets.

Fourth, and finally, one could appeal to the fact that position sense is only one source of information about limb location among several others, a position advanced by Wong (2014; in press). For example, efferent copies of motor commands will specify end points of actions, which then become estimates of current location after completion of the action. Similarly, tactile cues about contact of the limb with objects and surfaces provide clear information about limb location. And finally vision of the body also

provides clear information about body location. The distortions identified by Longo and Haggard (2010) relied on a laboratory situation which artificially isolated proprioceptive position sense independent of other cues for limb location. In real-life situations in which position sense is merely one cue among many for limb location, the distortions described above may pose relatively modest problems for skilled action. More generally, no sense is perfect, and multisensory integration of information across modalities allows the deficiencies of any individual sense to be compensated for by others.

The so-called 'distortion challenge' (Wong, in press) arises from the facts that (a) body representations underlying position sense are highly distorted (Longo & Haggard, 2010), and (b) that position sense is critically important for skilled action (Cole & Paillard, 1995). I have discussed four ways in which this apparent discrepancy might be addressed: (1) by questioning whether distortions are actually more problematic for motor control than well-established variable errors (Tillery et al., 1991), (2) by emphasizing that many uses of proprioception require only information about joint angles rather than absolute location, (3) by highlighting the extent to which motor commands specify movement endpoints rather than precise spatial trajectories (Polit & Bizzi, 1978), and (4) by identifying the diverse set of multisensory cues which complement proprioceptive position sense and may compensate for distortions (Wong, in press). These interpretations are clearly not mutually exclusive, and all may contribute to some extent in meeting the distortion challenge and accounting for the obvious fact of dexterous action despite the clear distortions in the body model underlying position sense.

Implications for the sensation of movement

I will conclude by discussing some implications of distorted body representations for understanding the sensation of movement. The first point I wish to emphasize is the extent to which such distortions are implicit, and outside of conscious awareness. As discussed above, Longo and Haggard (2010) argued that the distorted body model they described was distinct from the conscious body image given that no analogous distortions were found when participants selected the hand most like theirs from an array of hand images which had been stretched to varying degrees, ranging from extremely long and slender to extremely squat and fat. Though subsequent studies have shown that certain aspects of these distortions can be found in attenuated form with more explicit judgments (e.g., Longo, 2015d; Longo & Haggard, 2012), people are not generally aware of distortions in their representation of their hand.

That much of the operation of position sense and its role in motor control operates outside of awareness is also shown by the case of patient I.W. Though he re-learned to perform many types of actions, this required that he devote constant focus and attention to the position and orientation of his limbs. Thus, I.W. was forced to rely on conscious attentional resources to achieve functions which, in the presence of intact position sense, are accomplished automatically and outside of conscious awareness, as part of the cognitive unconscious (Kihlstrom, 1987).

So far, I have emphasized the relation of distorted body representations to unconscious mental processes. It is important, however, to note that while participants in the study of Longo and Haggard (2010) were not aware of the distorted perceptual maps which they were producing, they were of course aware of the response they were making on each trial. Moreover, the judgment was specifically of the felt location of a given landmark. Thus, the perception of bodily location which the body model is involved in computing certainly is accessible to conscious awareness, even if the nature

of the body model itself is not. The distortions of the body model are therefore not irrelevant to understanding our conscious experience of body position or movement.

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