Distortion of Mental Body Representations

Matthew R. Longo
Department of Psychological Sciences, Birkbeck, University of London

Address correspondence to:
Matthew Longo
Department of Psychological Sciences
Birkbeck, University of London
Malet Street, London WC1E 7HX
United Kingdom

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Abstract

Our body is central to our sense of self, and distorted body representations are found in several serious medical conditions. This paper reviews evidence that distortions of body representations are also common in healthy individuals, in domains including tactile spatial perception, proprioception, and the conscious body image. Across domains, there is a general tendency for body width to be overestimated compared to body length. Intriguingly, distortions in both eating disorders and chronic pain appear to be exaggerations of this baseline pattern of distortions, suggesting that these conditions may relate to dysfunction of mechanisms for body perception. Distortions of body representations provide a revealing window on basic aspects of self perception.

Distorted Body Representations in Health and Disease

Our body is the core of our sense of self and our personal identity. Distortions and misperceptions of the body are conspicuous features of numerous clinical disorders. In psychiatry, examples include body image distortions in eating disorders in which emaciated individuals feel overweight [1], body dysmorphic disorder in which people become fixated on some part of their body being horribly ugly [2], and body integrity dysphoria in which people desire to amputate healthy body parts [3]. Similarly, in neurology, examples include phantom experiences of amputated limbs [4], anosognosia for hemiplegia in which patients deny their inability to move [5], and somatoparaphrenia in which individuals deny ownership over body parts [6]. Other examples seem more bound to specific cultural or historical contexts, such as the ‘glass delusion’, widespread in 16th century Europe, in which people feared they were made of glass and would shatter [7].

The intimate link we have with our body could make it seem as if knowledge and experience of the body were immune to illusions and perceptual errors. Indeed, the English language makes the body a paragon of intimate knowledge and deep familiarity in phrases like knowing something “like the back of my hand”. A growing literature, in contrast, has shown that far from being specific to disease, distorted body representations are a basic part of ordinary cognitive life. Understanding these distortions provides a valuable window into the nature of mental body representations and their underlying mechanisms. It also holds promise in providing insight into the role of body distortions in diseases such as eating disorders and chronic pain, and how they might be treated.

Neural Maps and Body Cartography

Maps are ubiquitous in the brain, from retinotopic maps of visual space [8] to tonotopic maps of sounds [9], from cognitive maps of the environment [10] to semantic maps of conceptual structure [11]. The most conspicuous maps in the nervous system, however, are the body maps in primary motor and somatosensory cortex, the famous motor and sensory ‘homunculi’. Early studies involving direct electrical stimulation in animals [12] and humans [13] showed that the pre-central and post-central gyri contain organised maps of the contralateral body serving motor and sensory functions, respectively. Single-unit electrophysiological recordings from monkeys identified even finer structure, showing that primary somatosensory cortex includes four distinct body maps [14]. More recent fMRI mapping studies have described more than a dozen distinct maps throughout parietal and frontal cortex [15]. Studies in animals [16–18] and humans [19,20] indicate they are present from early in development.

Famously, these homuncular maps are massively distorted, the amount of cortex devoted to body parts being related to sensitivity, rather than physical size [13,21]. This is reflected in the familiar textbook figure of the homunculus with enormous fingers and lips, and tiny torso and legs. How do these distortions relate to function? The disproportionate processing resources representing a limited set of skin regions (fingertips, lips) allows us to perceive the world in ways we could not were sensitivity homogenously mediocre across the body.

Analogously, by facilitating extraordinary dexterity for specific body parts (hands, vocal tract), we can perform actions that we couldn't with homogenous dexterity.

By probing distortions of maps we can gain deep insight into their nature and function (Box 1). Consider the famously distorted London tube map (Figure 1). The ways the tube map distorts the actual geography of London are direct consequences of the map's purpose. By investigating the tube map's distortions, we can learn a great deal about its function of helping commuters travelling by train. Analogously, by investigating the distortions of mental body maps, we can learn about their roles in psychological life. Of course, the tube map is a deliberate creation of a mapmaker (Harry Beck), whereas mental body maps are a result of evolutionary and developmental processes. Despite this fundamental difference, each map emphasises certain features over others. Studying a map's features can thus give us a rich window into its underlying functions.

Distorted Body Representations in Touch

In the 19th century, Ernst Weber [22] described a curious illusion which now bears his name (*Weber's illusion*). Moving the two points of a compass across the skin, the perceived distance between them changed depending on the sensitivity of the skin surface. They felt farther apart on more sensitive surfaces. Numerous subsequent studies have replicated this systematic relation between perceived tactile distance and tactile spatial sensitivity [23,24]. As tactile acuity is itself linked to cortical magnification in somatosensory cortex [25], the illusion can be thought of as a perceptual reflection of the distortions of the Penfield homunculus.

More recently, tactile distance illusions have been described as a function of stimulus orientation on individual skin surfaces (tactile distance anisotropy). For example, pairs of touches oriented across the width of the hand dorsum were perceived as about 40% larger than the same distance oriented along hand length [26]. Similar distortions have been reported on the palm [27–29], forearm [30,31], thigh [31,32], shin [33], feet [34], and face [27,28,35]. One study [36] found analogous anisotropy in temporal perception: the duration between two taps feels longer when separated across hand width than length. Intriguingly, while the magnitude of anisotropy varies, the direction of anisotropy is consistent: distances oriented with body width are perceived as larger than those oriented with body length or height. The one place this has not been found is the torso, with no apparent bias on the belly [31,37] and an opposite effect on the lower back [38,39].

Growing evidence suggests that tactile distance biases are modulated by illusions of body size [24,40,41] and tool use [42,43]. One study [41] used an audio-tactile mismatch to create the illusion of an elongated arm, finding corresponding elongation of perceived tactile distance on the arm. There is also evidence for categorial perception of tactile distance across body-part boundaries at joints [30,44–46]. Intriguingly, this is also true for speakers of Croation [46], which uses a single word (*ruka*) encompassing hand and arm, and thus does not lexically mark the wrist boundary as English does.

Despite these links between tactile distance perception and high-level body representations, there is also evidence that distortions relate to more basic aspects of somatosensory organisation. Tactile distance aftereffects occur following adaptation to large or small tactile distances [47], suggesting the distance between touches is a basic feature coded by the somatosensory system. Importantly, these aftereffects showed several features of "low-level" aftereffects, including orientation-specificity, location-specificity, and lack of contralateral transfer, suggesting distance is coded at relatively early stages of somatosensory processing.

As noted above, there is a systematic relation between the perceived distance between touches and spatial acuity. Intriguingly, this pattern also holds with respect to the tactile distance anisotropy distortions described above, given that tactile acuity is also higher across the width of limbs than along length [22,48]. This is mirrored by the geometry of receptive fields of somatosensory neurons. In addition to being smaller on sensitive skin regions [21], receptive fields on the hairy skin of the limbs are generally oval-shaped with the long axis aligned with the proximo-distal limb axis [49]. One approach to interpreting these effects is the 'pixel' model [26,50] in which receptive fields in a somatotopic map are treated as pixels in a two-dimensional array and perceived distance is calculated as the number of pixels separating activation peaks (Figure 2). This model can account for both the classic form of Weber's illusion, since sensitive skin surfaces have a larger number of small receptive fields than less sensitive surfaces, and also for anisotropy within a skin surface, since the orientation aligned with the short axis of the receptive fields a larger number of thinner receptive fields than the long axis.

On the pixel model, distortions of tactile space should be geometrically coherent, in that they should be well-characterised by simple deformations, such as stretches. One study [28] tested this by having participants judge the distance between pairs of touches at several orientations. If distortions reflect a simple stretch of tactile space, perceived distance should vary predictably as a sinusoidal function of stimulus orientation. This pattern was apparent across several skin regions, suggesting that spatial distortions of touch reflect a geometrically-simple stretch of tactile space. Interestingly, this structure is preserved in focal dystonia [51], despite these patients' motor difficulties. This is strikingly different from the visual horizontal-vertical illusion, which is maximal for stimuli rotated slightly clockwise or counter-clockwise from vertical [52], and thus cannot reflect a coherent stretch of visual space.

Other work has mapped distortions using multidimensional scaling (MDS) to reconstruct perceptual and neural maps of tactile space. MDS reconstructs the latent spatial structure under a matrix of distances or dissimilarities. While generally used in psychology and cognitive neuroscience as a visualization tool to understand complex datasets, MDS can also be used to reconstruct perceptual spaces if applied to a matrix of judged distances. In one study [53], participants judged the distance between pairs of touches. By stimulating every pair of points in a 4x4 grid, a perceptual distance matrix was obtained, and MDS was used to construct a 2-dimensional perceptual map of the skin. These maps were highly distorted and stretched compared to actual skin shape. Another recent study [54] applied this logic to reconstruct neural maps of tactile space by applying MDS to representational dissimilarity matrices obtained using functional magnetic resonance imaging (fMRI) following stimulation of several locations on the hand (Figure 3). Organised maps of the skin were reconstructed from primary somatosensory and motor cortices. These neural maps of the skin were distorted similarly to perceptual maps, suggesting distortions arise from the basic organisation of early sensorimotor cortex.

Distorted Proprioceptive Body Maps

Similar distortions have been described in tasks measuring proprioceptive localisation of body parts in external space. Several sensory signals provide information about body posture, including receptors in joints, muscle spindles, and skin. Each of these signals, however, provides information about the *angles* of joints, rather than absolute information about bodily location, analogous to a GPS signal. To determine the location of a body part such as the finger, joint angles must be combined trigonometrically with information about segment lengths between joints. Such length information is not specified by immediate sensory signals, suggesting it comes from a stored representation of body size and shape (Figure 4) [55].

One method to isolate and measure this stored body model involves having participants point to multiple landmarks on their occluded hand [56]. By comparing the relative location of landmarks, perceptual maps of hand size and shape can be constructed. The logic of this method is that while the absolute perceived location of an individual landmark will be influenced by a range of factors, many of these will affect multiple landmarks in the same way. For example, misperception of the angle of the elbow joint will result in systematic mislocalisations of both the knuckle and tip of the index finger. By comparing the *relative* judged locations of multiple landmarks (e.g., the knuckle and tip of each finger), the representation of the internal metric configuration of the hand can be estimated. These maps were systematically distorted, in a stereotyped way (Figure 4), showing: (1) overestimation of hand width, (2) underestimation of finger length, and (3) a gradient across fingers with least underestimation of the thumb and most of the little finger.

This method requires that the body part mapped has discrete landmarks with known verbal labels, a major limitation. Other studies have therefore extended this approach to obtain maps based on localisation of points cued by touch or by a visual mark appearing on a body part image [57,58]. These maps show similar overestimation of hand width whether based on localisation of visual [57,58] or tactile [57] cues.

Subsequent studies extended this paradigm in several ways. The distortions are not specific to the hand, but occur on the forearm [59], leg [33], and face [60,61]. Similarly, distorted maps occur for proprioceptive imagery when participants simply imagine their hand underneath the board [62,63]. These imagery results are consistent with findings that people with a lack of somatosensory signals show comparable distortions [64], as did a woman with congenital limb absence [65]. There is also long-term plasticity of these maps in people with specific expertise, such as skilled magicians [63] and elite basketball players [66]. Most importantly, recent studies have investigated the role of the distorted body model in active motor control [67,68]. By having participants move landmarks on their hand to the location of visual targets, they showed that active motor control is not immune to these distortions. Nevertheless, the magnitude of distortions was reduced, suggesting a partial correction used to guide action.

The origins of these distortions remain uncertain. Some authors [56] have emphasised similarities between proprioceptive maps and distortions in the somatosensory system. For example, overestimation of hand width versus length mirrors anisotropies in tactile acuity, tactile distance perception, and RF geometry described above, while the gradient across fingers mirrors differences between fingers in tactile acuity and cortical magnification [25]. Subsequent studies have suggested that more general factors may also contribute [69–74]. For example, similar distortions occur when participants localize landmarks on non-body objects based on visual memory [69,71]. Other studies report systematic conceptual misunderstanding of the location of landmarks such as knuckles, which could (at least partly) explain distortions such as underestimation of finger length [70,72,74]. Recent research suggests that a combination of body-specific and domain-general factors may contribute [75]. The nature of these domain-general factors remains unclear, but one possibility would be a bias to represent long, thin objects as less elongated than they really are. Similarly, basic aspects of the way the limbs are perceived visually may affect their representation, such as the horizontal-vertical illusion, or the fact that the arms tend to be seen in foreshortened perspective.

Distortions of the Conscious Body Image

The concept of 'body image' has been used in various ways in both neurology and psychiatry, incorporating a diverse range of concepts, attitudes, and percepts. Here, I will refer to the body image as the consciously experienced feeling of the body, in terms of size, shape, and physical composition. In reflecting our conscious experience of the body, the body image is distinct from the more implicit body representations underlying touch and proprioception described in the previous sections. Much of the work in this area has focused on the distorted body image of patients with eating disorders, widely studied since the 1970s (for a recent meta-analysis, see [76]). Numerous paradigms have been developed to assess perception of body size, such as the moving caliper, video distortion, and the image marking procedure. These tasks can be categorized into two broad groups [77]: *depictive methods* (e.g., video distortion) in which participants compare their own body to a visual image of a body, and *metric methods* (e.g., moving caliper) in which participants compare the metric properties of their body to non-body standards. It has been noted that while patients overestimate body size compared to controls, controls nevertheless show absolute overestimation of body width compared to actual body size, at least for metric methods. As a typical example, one study [78], using the moving caliper method, found that healthy participants overestimated waist width by 24% and chest width by 23%. Notably, there was no overestimation of the width of a rectangular box, suggesting overestimation was not a procedural artefact, and was body-specific.

Such effects are common in the eating disorders literature, but have generally been treated as a methodological difficulty, rather than an interesting phenomenon. Recent research has investigated these effects in more detail. Some studies [79,80] had participants localize body parts relative to a fixed landmark. There was strong overestimation of the width of both the entire body [79] and the face [80]. Another study [77] measured perceived finger length and hand width by having participants compare each body part to a visually-displayed line, finding distortions qualitatively similar to – but quantitatively smaller than – distortions of proprioceptive maps, described above. Similar distortions occur on other body parts, including the foot and lips [81]. Intriguingly, similar distortions occur for manipulable objects (e.g., mobile phone), but not non-manipulable objects (e.g., cactus) [82].

Other studies have similarly demonstrated distortions in explicit judgments of body size. In one study [83], participants adjusted a tape measure to indicate perceived arm length, with right-handed people judging their right arm longer than their left. In other work [84], participants judged the length of several body parts in terms of multiples of their own hand length, finding large and systematic distortions. Intriguingly, the relative perception of size across body parts correlated with tactile sensitivity, with sensitive body parts, such as the hand, most strongly underestimated. They suggested that perceived body-part size is inversely proportional to cortical magnification as part of a process of 'reverse distortion' to perceptually correct for homuncular distortions to achieve tactile size constancy.

Most existing methods for measuring perceived body size and shape involve comparing the body to a 1-D standard (metric methods) or a 2-D image (depictive methods), ignoring that we experience our body as a volumetric, 3-D object. A handful of recent studies have thus begun to investigate the body image in 3-D. One study measured perceptual distortions of 3-D finger size, having participants judge whether each finger would fit through rings of different sizes [85]. The sizes of the non-thumb fingers were underestimated, a pattern which decreased from the index to little finger. Another study [86] adapted the paradigm of [84], described above, to investigate distortions in perception of body-part volume. There was a qualitatively different pattern of distortions than for length, with hands and arm volume overestimated compared to the leg and torso. A final study investigated perceived weight of individual body parts, and how this is affected by vestibular cues to gravity [87]. Experimental alterations of gravity using a short-arm centrifuge and parabolic flight produced rapid and systematic changes in the perceived weight of the head and hands.

Distorted Body Representations and Psychological Wellbeing

The link between distorted body representations and psychological distress is clear from the clinical literature on conditions such as anorexia [1] and body dysmorphic disorder [2]. This connection is also clear, however, outside of clinical contexts. Experimental induction of low mood increases perceived body width [88,89]. Another study found increases in perceived body width when women with bulimia nervosa were forced to eat or to weigh themselves [90]. There is also evidence that state anxiety increases in women with anorexia when asked to judge body size [91,92].

More recent studies have attempted to alter perceived body size directly, using virtual reality techniques to experience embodiment over more obese bodies [93–95]. One study [93] induced illusory body ownership of bodies either thinner or more obese than the participant's actual body. Participants wore a head-mounted display showing video from a camera mounted where the head would be on a mannequin, giving a first-person perspective of the mannequin body. Synchronous touch was applied to the abdomen of the participant and mannequin, providing multi-sensory signals that the body was the participant's own. Ownership over the slim mannequin increased self-reported body satisfaction. Another study [95] using fMRI showed that these changes in body satisfaction are linked to altered functional connectivity between the right intraparietal cortex, an area long linked to the body image, and regions involved in affective processing, including the anterior insula and anterior cingulate cortex. These effects of embodying obese and thin bodies fit with studies showing widespread cognitive effects of embodying bodies which differ in characteristics including age [96,97], race [98], and visibility [99,100].

Two recent studies [101,102] measured individual 'self portraits' using reverse correlation, a data-driven method for reconstructing internal representations of categories. On each trial, the participant sees two images of a base face with random noise added, and judges which looks most like themselves. Averaging these images produces a visual depiction of the participant's internal representation of their own face. In one study, participants whose self portraits were rated more negatively by independent raters showed lower self esteem [101]. Another study [102] also used reverse correlation to construct self portraits of participants' faces, which showed substantial similarity to participants' actual faces, both as judged by external raters and by a deep neural network trained on face recognition (OpenFace). Nevertheless, the self portraits also deviated from actual face shape. Critically, the magnitude of these distortions predicted participants' social self-esteem. The more distorted a person's self portrait, the lower their self-esteem. In another experiment, a similar technique was used to construct self portraits of the whole body using images of body silhouettes. Overestimation of body width in these body self portraits were correlated with bodily self-esteem. Together, these results indicate that distortions in people's internal body image are related to more psychological conceptions of attractiveness and self-esteem.

Collectively, existing evidence suggests a complex relationship between body perception and mental wellbeing, with bidirectional causal influences. Both appear to be influenced by a range of factors, both high-level factors such as anxiety [92] and memory [103], as well as low-level influences from basic somatosensory organisation, as described above. This raises the possibility that interventions targeted at manipulating distorted body representations may have useful therapeutic potential.

Distorted Body Representations in Disease

As discussed above, bodily distortions are a salient feature of many clinical disorders, as diverse as schizophrenia [104], arthritis [105], spinal injury [106], and obesity [107,108]. Here, I focus on recent developments in two specific cases, eating disorders and chronic pain. In eating disorders, recent work has moved beyond classic body size estimation tasks, to investigate systematically the ways in which bodily perception is abnormal in these patients. Similar overestimations of body width occur in tasks that do not require explicit judgments of body size, including passing through apertures [109,110], judging whether objects will collide with the body [111], or imagining tracing the body's contour [112]. Patients with anorexia also show abnormal tactile processing, overestimating tactile distances on both the hand and belly compared to controls [113–115]. This overestimation on the belly appears specific to the horizontal body axis [115]. Similarly, women with anorexia overestimate the width of elliptical stimuli on the fingertip [116]. Recent work has investigated whether multisensory embodiment illusions using virtual reality can alleviate these distortions, with mixed results [117–119].

Distorted body representations are also important in chronic pain, which involves a range of disruptions to body perception and somatosensory processing, for example in complex regional pain syndrome (CRPS) [120,121] and low-back pain [122]. When CRPS patients with hand pain choose from an array of hand images the one most like their own, they chose hand images wider and squatter than their actual hand [121]. Another study of chronic back pain, in contrast, found that patients experienced their back as shrunken, and even as difficult to find [122], indicating that not all forms of pain affect body perception in the same way. Other studies showed that experimental manipulations of perceived body size can alleviate chronic pain [123–126]. One study [125] used a mediated virtual-reality system (MIRAGE) to let CRPS patients alter the visual appearance of their hand to match its desired appearance, producing strong reductions in pain intensity, which were sustained over two weeks.

It is striking that the distortions of body perception seen in both eating disorders and in at least some forms of chronic pain involve overestimation of body width, given that qualitatively similar distortions are ubiquitous in healthy individuals, as described above. This raises the possibility that exaggeration of biases that are part of healthy cognitive life, or overweighting of distorted somatosensory signals over more veridical visual signals, may contribute to the emergence of these conditions [127,128]. It remains unclear exactly how this happens. One possibility is that distortions typically found on one body part (e.g., the arm) might transfer to other body parts in which they are not typically found (e.g., the belly). Analogous transfer of somatosensory plasticity between body parts has been reported in numerous contexts [129,130]. Another possibility is that distortions that are typically part of the background of mental life become drawn into conscious awareness, potentially becoming objects of fixation or distress.

Concluding Remarks

The London tube map is an icon of elegant design, and an indispensable tool that has helped millions of commuters and visitors navigate the city. The elegance and utility of the tube map is due in large part to the particular way in which it distorts the true geography of London, allowing it to emphasize features and clarify patterns that would otherwise get lost in the complex reality of the metropolis. Though not designed by a mapmaker, the same principles are true of mental body maps. While distorted body representations are a conspicuous feature of many clinical conditions, they are not specific to disease. Distortions of body perception, in contrast, appear to be a normal part of healthy mental life. While much remains to be learned about these distortions (see Outstanding Questions), some general principles have begun to emerge. There is a quite general tendency for body width to be overestimated, which appears across several perceptual domains. Importantly, this bias found in healthy individuals appears to be exaggerated in conditions such as anorexia and chronic pain. This suggests that these clinical disorders may relate to dysfunctional processing of bodily signals. Future research should aim to understand more clearly the link between distortions found in health and in disease, which offers promise for understanding the causes of these disorders and potentially identifying novel therapeutic approaches. Notably, illusions used to alter body perception have recently shown promise in treating both anorexia [117,119,131] and chronic pain [124,125].

The functional role of distortions remains poorly understood. Magnification of some body parts compared to others has clear adaptive value in allowing extraordinary sensitivity and dexterity of specific body parts, such as fingertips and lips, that facilitates skilled hand use and language. Other distortions may provide a counterbalancing bias in the opposite direction, helping to undo distortions due to magnification to achieve perceptual constancy [84]. The function of other distortions, such as the general overestimation of body width versus length, is less clear. Speculatively, one possibility is that this serves to increase individuation of the fingers, which are organised across the width of the hand, facilitating dextrous hand actions. Alternately, it is possible that it reflects differential post-natal growth rates of different body axes on neural maps laid down in the fetal brain. It also possible that distortions may arise as a result of spatial and perceptual biases that exist for other reasons entirely.

Several recent studies have suggested that even in entirely non-clinical samples, distorted body representations relate to several aspects of psychological wellbeing, including body dissatisfaction [93,95] and self-esteem [101,102]. Thus, while distortions may be a ubiquitous part of healthy cognitive life, they may also represent a risk factor for mental health issues. Future studies should aim to identify more precisely how distortions result in mental distress and what factors may mitigate this.

A final crucial issue concerns what factors contribute to the emergence of distortion in the first place. The body is perceptually unique in that we experience it both from the inside, as the seat of our sensations and the reference of first-person experience, but also from the outside, as a physical object in the world like any other [55]. It is therefore likely that body representations are shaped by a combination of factors specific to the body and others common to object perception more widely. Recent studies have started to disentangle these processes [69,72–74,81,82].

Box 1: Distortions as a reflection of a map's function

Research in geography shows that distortion is a ubiquitous – even essential – feature of maps. As Peter Barber, Head of Map Collections at the British Library, says [132], "There is no such thing as an accurate map; there is bound to be distortion, depending on what purpose it sets out to serve."

All maps lie. And these lies produce distortions, spatial and otherwise. The lies that maps tell, however, are not mendacious, nor are they incidental or haphazard. On the contrary, the lies that maps tell – and the distortions that arise as a result – are profound reflections of the functional essence of the map itself. Indeed, in his book *How to lie with maps* [133], Mark Monmonier makes this point clear, writing that "Not only is it easy to lie with maps, it's essential."

Research in geography has emphasised that distortion is an inescapable aspect of any map. As a simplified representation of a complex object, a map must necessarily emphasise some features at the expense of others. The distortions of maps are thus neither mere curiosities nor meaningless accidents, but profound reflections of the fundamental purpose of the map. This principle is as true for mental body maps as for geographic ones.

Image not shown for copyright reasons

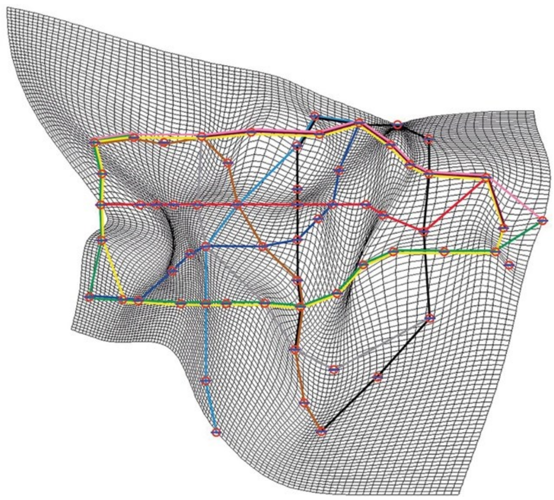

Figure 1: A case study - The London tube map. Harry Beck's iconic 1933 map of the London Underground (left) famously distorts the actual geography of London. The right panel shows the distortions of the modern tube map (central London only) using a D'Arcy Thompson style transformation grid [134]. What clues to the map's function do we get from studying its distortions? First, distances between stations are massively overestimated in central London compared to outlying areas – central London is *magnified*, exactly like the fingers and lips in the Penfield homunculus. This reflects the mapmaker's expectation that more people will be interested in central London than the suburbs. Second, the locations of stations are displaced so as to align stations on the same tube lines. This emphasises the *connectivity* of stations, at the expense of distorting their *proximity*. This makes sense given the map's function of helping passengers riding the tube, but would be a disaster for someone navigating by foot. Pedestrian maps of London are designed very differently. The distortions are not errors, but intimate reflections of the map's function. The distortions thus provide a revealing window into the functional essence of the map.

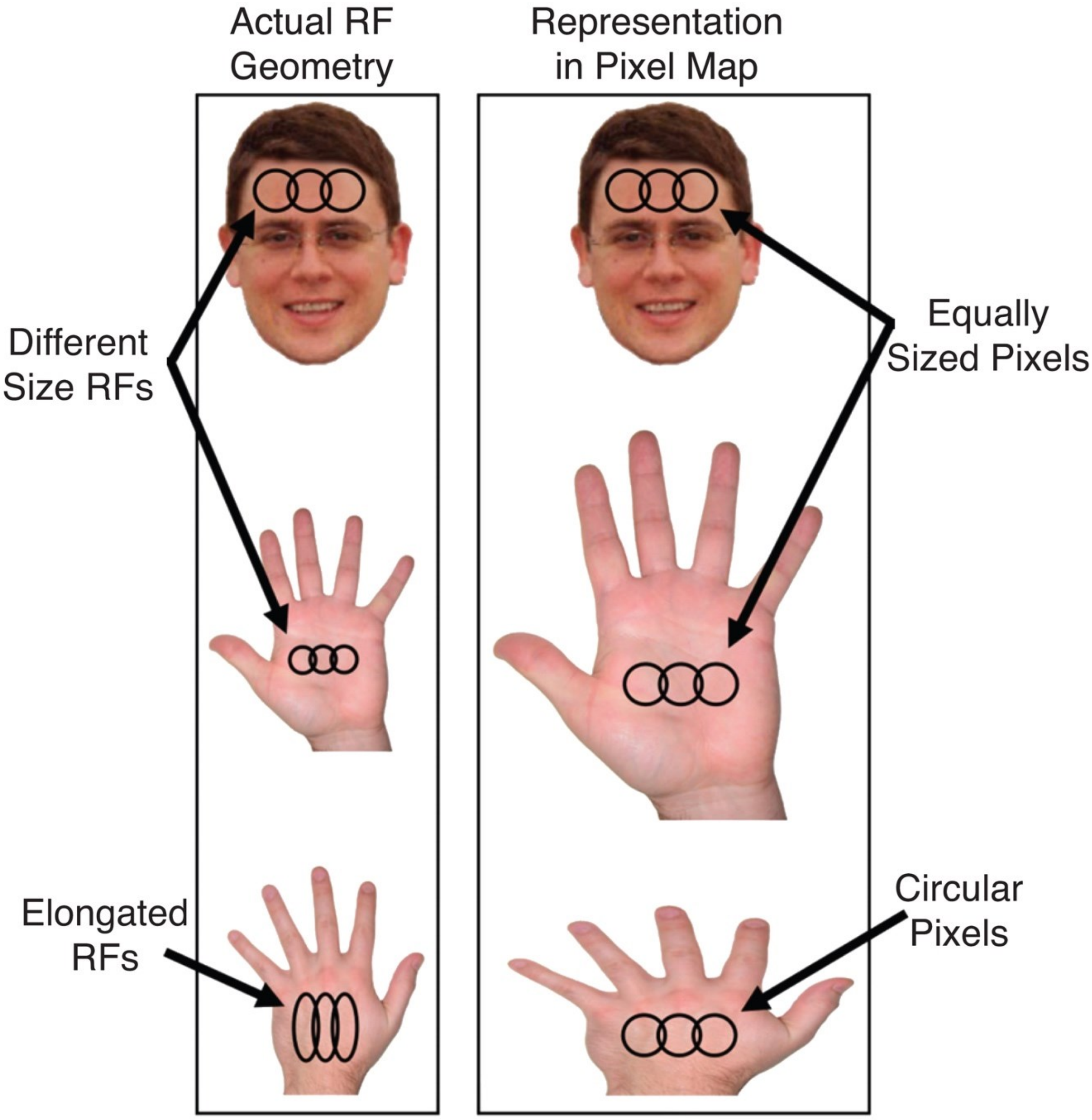

Figure 2: The pixel model of tactile space perception. The pixel model [26] accounts for a range of distortions of tactile distance perception. The core idea is that receptive fields (RFs) are the basic unit of distance perception, which essentially involves counting of RFs between two stimulated activation peaks. Since RFs are smaller, and correspondingly more densely spaced, on highly sensitive skin surfaces (e.g., the hand) compared to less sensitive surfaces (e.g., the forehead), the same physical stimulus will cover more pixels in the former case. This corresponds to the classic form of Weber's illusion in which tactile distances feel larger on more sensitive skin surfaces. Since RFs on the limbs are elongated parallel to the long axis of the limb, RFs are smaller, and more densely spaces, in the medio-lateral limb axis than in the proximo-distal limb axis. This corresponds to the tactile distance anisotropies in which tactile distances feel larger when oriented across the width of the limb than along its length.

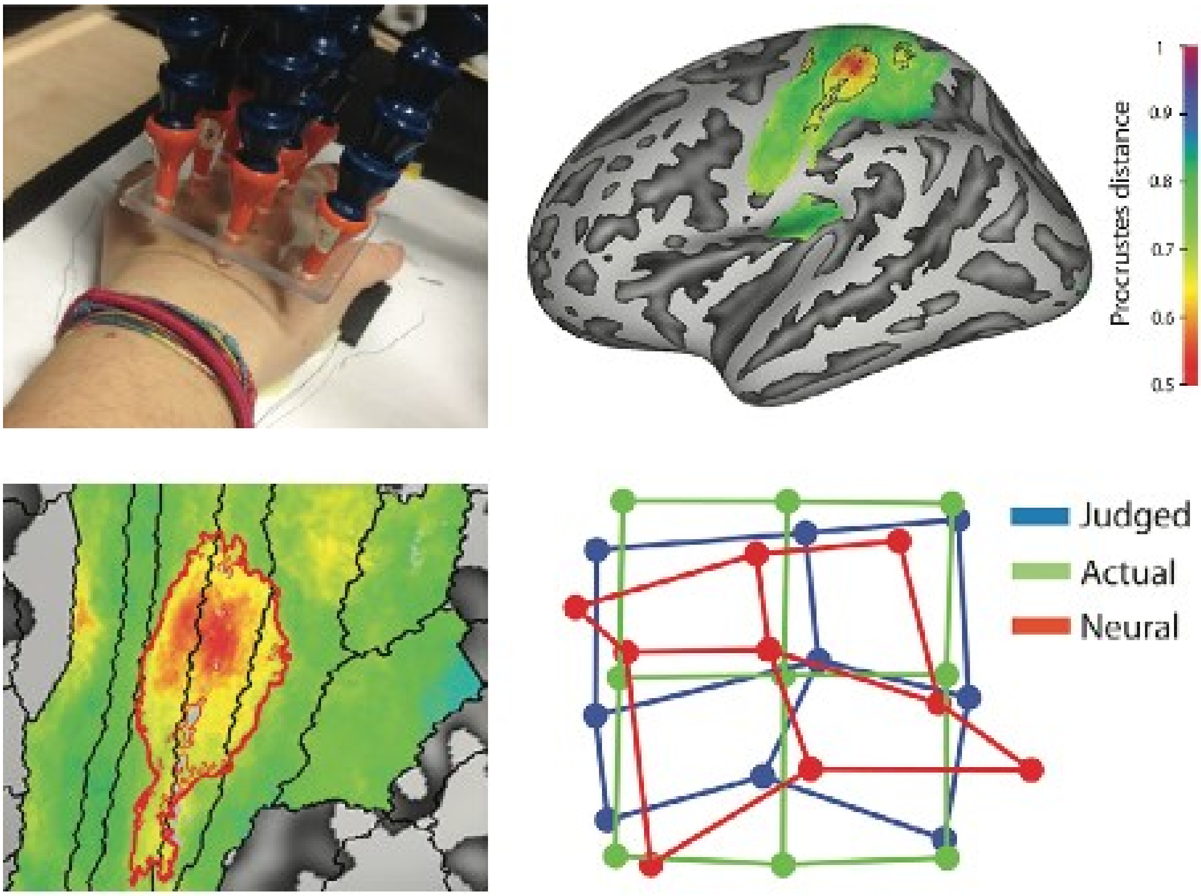

Figure 3: Using multidimensional scaling (MDS) to reconstruct neural maps of tactile space. A recent study used representational similarity analysis (RSA) of fMRI data to reconstruct maps of tactile space in different regions of the brain [54]. MDS is a statistical method that transforms a matrix of distances between items into a set of Cartesian-coordinates for those items in space. For example, given a matrix of the flying distances between each pair of five European cities (*top left*), MDS produces a map of Europe (*top right*). The same logic can be used to produce perceptual maps by obtaining a matrix of perceived distances between stimuli [53] or neural maps by obtaining a representational dissimilarity matrix (RDM) quantifying how dissimilar distributed patterns of brain activity elicited by each stimulus are [54]. To generate neural maps, tactile stimuli were delivered using an fMRI-compatible air-puff stimulator (Dodecopus [15]; shown in inset at bottom left). Nine locations on the right hand dorsum were stimulated in a 3x3 grid. Within each region of interest, a representational dissimilarity matrix was constructed based on the pairwise Euclidean distance between the patterns of activations produced by stimulation of each location. MDS was then used to reconstruct a 2-D maps of the nine locations, and the dissimilarity of this maps to the true layout of the skin was quantified. A searchlight analysis constructed maps across brain areas to identify brain regions from which the true layout of the skin could be reconstructed from the pattern of representational dissimilarities (*bottom left*). The clearest reconstruction of the skin was in the primary somatosensory cortex, straddling the border between Brodmann's areas 3b and 1. *Bottom right*: grand average maps of the actual stimulated locations on the skin (green), perceptual maps reconstructed from MDS on tactile distance judgments (blue), and neural maps reconstructed from MDS on representational dissimilarity matrices in areas 3b/1. Similar distortions were found for perceptual and neural maps, with hand width stretched by 47% in each case.

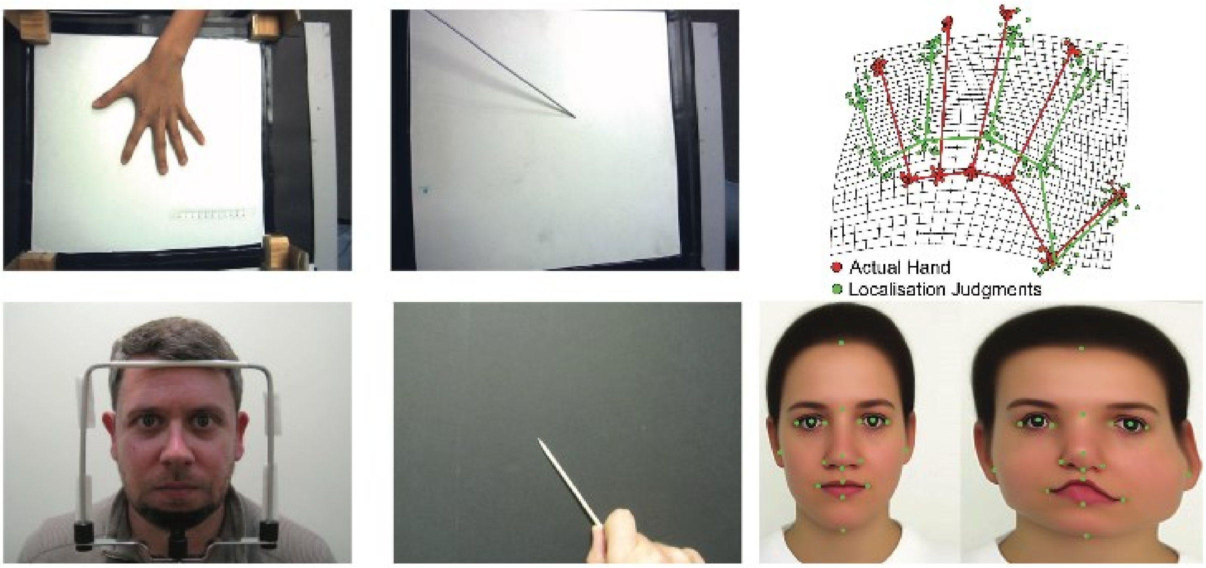

Figure 4: Distortions of proprioceptive maps. *Top left*: proprioceptive afferent signals provide information about joint angles (e.g., θ_s and θ_t), but determining the absolute location of the hand compared to the shoulder also requires information about body size (e.g, L_{ua} and L_{fa}). *Top right*: The procedure used to measure perceptual hand maps based on proprioceptive localisation [56]. The participant places their hand flat on a table, and then localises different parts of their hand by pointing on an occluding board placed above the hand. Proprioceptive hand maps are constructed by focusing on the distances between judgements for different landmarks (e.g., RLif), ignoring absolute errors of localisation (e.g., E_k and E_{ft}). Distortions can be assessed by comparing represented and actual hand maps (e.g., RL_{if} versus L_{if}). *Bottom left*: grand-average perceptual maps placed into Procrustes alignment with actual hand shape. There is strong overestimation of hand width relative to length. *Bottom right*: The similar procedure used to measure perceptual face maps [61]. the face at left shows the average actual structure of participants' faces, while the face at right shows the average structure of perceptual maps. As with hands, there was strong overestimation of face width relative to height.

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