CHAPTER 3

On Feeling and Reaching: Touch, Action, and Body Space

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3.1 INTRODUCTION

One of the most important functions of an organism is the ability to move around the environment and to interact with objects within the environment. Spatial information is crucial here. For example, we need to know where objects are on a cluttered table in order to be able to move toward and grasp that ubiquitous cup of coffee while avoiding spilling the jug of juice. Importantly, we need to know where these items are with respect to our own body in order to perform these movements accurately. This requires spatial information about our own body parts, from proprioception and touch as well as visual information about the items in the environment. In turn somatosensory input is not just used for guiding actions, but can also directly provide spatial perceptual information about the environment through haptic exploration, as well as about our targets on our own body. These spatial somatosensory perceptual experiences are not necessarily veridical, but can be prone to specific distortions. In healthy participants, distortions in somatosensory experience may tell us something about the underlying spatial representations. However, perceptual somatosensory experience can also be disturbed in clinical populations. In this chapter I start by providing an overview of the functional organization of the somatosensory system. Somatosensory input is important for providing a representation of our body as well as for haptic exploration of external objects. Both are reviewed next. A representation of the space surrounding our body, the peripersonal space, has been linked to body representations as well as goal-directed action and is described next. Finally, spatial processes underlying the guidance of reaching and grasping are discussed.

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3.2 SOMATOSENSORY PROCESSING FOR PERCEPTION AND ACTION

Over the past two decades a dominant model for visual cortical processing has been the two visual streams model, in which visual information is processed along two separate stream of cortical processing, the ventral stream and the dorsal stream (see Section 3.6 and grasping and Chapter 2). The ventral stream is supposed to be involved in visual processing for perception and recognition, while the dorsal stream processes visual input for the guidance of action (Milner & Goodale, 2008). A similar functional subdivision has been suggested for the somatosensory system, although the anatomical subdivision is much less clear (see Box 3.1)

BOX 3.1 Somatosensory Systems of the Brain

The somatosensory system is concerned with input from different submodalities such as touch, proprioception, sensitivity to hot and cold, pain and itch. Receptors within the skin, muscles, joints, and tendons convey information about these submodalities. Information from these receptors in all body parts except the face is transmitted first to the dorsal side of the spinal cord. Two ascending pathways convey the input to the brain (Fig. 3.1). The dorsal column, or medial lemniscal system carries discriminative tactile input and proprioceptive information through large myelinated fibers. The spinothalamic or anterolateral system mainly carries temperature information, pain, and affective tactile input. Both fiber systems cross to the contralateral side within the spinal cord, but at different locations. While the anterolateral system crosses about one or two spinal nerve segments above where it entered the spinal cord, the medial lemniscal system crosses much higher at the level of the medulla. Both project to different nuclei within the thalamus from which input is conveyed mainly to the primary somatosensory cortex within the anterior part of the parietal lobe. The primary somatosensory cortex contains a somatotopic maps of the contralateral half of the body. Body parts with a higher receptor density such as the hands or face are represented in a larger part of the cortical surface. Response properties within the primary somatosensory cortex closely resemble the somatosensory stimulus and its location, especially close to the thalamic input. Damage to the primary somatosensory cortex results in a loss of tactile and proprioceptive perception for the contralateral half of the body (hemianaesthesia, see Table 3.1). The insular cortex is another area that receives some somatosensory input. It is important for processing affective touch conveyed through small unmyelinated c-tactile fibers, but also

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BOX 3.1 Somatosensory Systems of the Brain—cont'd

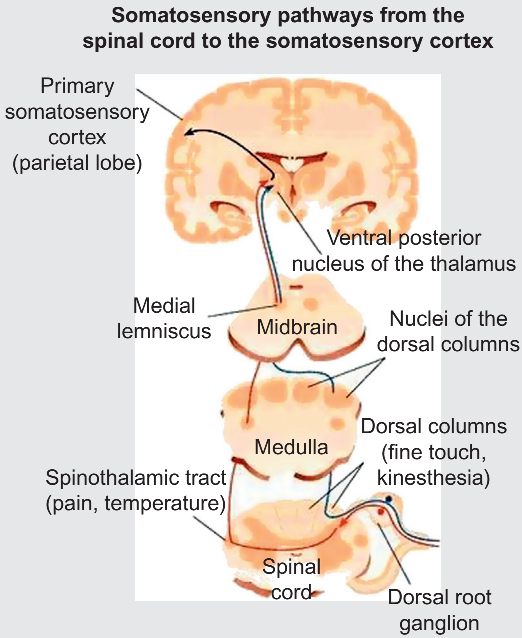

Figure 3.1 An overview of the two ascending sensory pathways, the dorsal column and the spinothalamic tracts that convey somatosensory input to the brain. *From van Stralen, H. E., & Dijkerman, H. C. (2011). Central touch disorders.* Scholarpedia *6(10), 8243.*

for pain perception and for sensitivity to hot and cold. Again, input is mainly projected contralaterally and at least for affective touch it is somatotopically represented (Bjornsdotter, Loken, Olausson, Vallbo, & Wessberg, 2009). Higher order somatosensory processing involves a more distributed network including the secondary somatosensory cortex (SII), located in the parietal operculum, the posterior parietal cortex, and the insular cortex. Responses to somatosensory input can also be found in premotor areas and in higher order visual areas such as LOC. Higher order processes can involve extracting features about and recognizing external stimuli such as objects in the environment. This mainly involves SII as well as posterior parietal areas. On other hand, somatosensory input also contains information about the body and contributes to a conscious bodily experience. Here the posterior parietal cortex, the premotor cortex, and insula play an important role. The posterior parietal cortex has been found to be involved in spatial and structural aspects of body

(*Continued*)

BOX 3.1 Somatosensory Systems of the Brain—cont'd

representations, while the insula is important for affective aspects of body representations. Activity in the premotor cortex has been linked to the feeling of body ownership (Ehrsson, Spence, & Passingham, 2004). Some authors have suggested a distinction between somatosensory processing for perception and action in higher order areas (Dijkerman & de Haan, 2007) while others suggest that a network of interrelated areas subserve various aspects of bodily experience, the body matrix (Moseley, Gallace, & Spence, 2011).

(Dijkerman & de Haan, 2007). Like the visual system, evidence for this functional dissociation comes from studies with neurological patients and from studies using illusions in healthy participants. A first piece of evidence came from studies of patients with "numbsense," a tactile equivalent of blindsight (Paillard, Michel, & Stelmach, 1983; Rossetti, Rode, & Boisson, 1995) (see also Table 3.1). These patients were unable to consciously detect tactile stimuli on their insensate hand, but were nevertheless able to localize them with above chance accuracy when making direct pointing movements toward them. Tactile information apparently could not reach the perceptual detection centers, but could have access to motor areas that involved in reaching movements. Paillard (1999) contrasted this with patient GL who suffered from peripheral deafferentation of the large myelinated fibers conveying discriminative touch and proprioceptive input to the brain. When touched with a cold stimulus, GL could localize the stimulus on a drawing of the hand (eg, intact perceptual localization), but when the hand was moved to a different location, was impaired when trying to point to the touch location. In a more recent study, Anema et al. (2009) also observed double dissociation between tactile localization when pointing directly to the target stimulus or localizing the touch on a drawing of the hand. Both patients were able to consciously detect the tactile stimulus, but nevertheless differed on their ability to localize it depending on the mode of response.

Dissociations between somatosensory processing for perceptual purposes and for the guidance of action have also been reported in healthy participants. In an early study, Westwood and Goodale (2003) showed that haptic size contrast illusions affected perceptual size estimates, but not grip aperture during grasping. Anema, Wolswijk, Ruis, and Dijkerman (2008) reported a difference in grasping and size estimation responses for

Table 3.1 An overview of different somatosensory and body-related functional deficits

Deficit	**Description**	**Affected function**
Hemianaesthesia	Loss of somatosensory function on one half of the body	Primary somatosensory function
Numbsense	Inability to detect tactile stimuli, while still being able to make movements toward them	Somatosensory perception
Somatoparaphrenia	Patients deny ownership over a body part and often attribute it to someone else	Body ownership
Misoplegia	Abnormal hatred toward a body part	Body affect
Finger agnosia	Impairment in identifying the fingers despite a preserved ability to use them	Body structure
Left–right disorientation	Impairment in the identification of the left and right sides of one's own, but also someone else's body	Body structure
Autotopagnosia	Patients are unable to point to their own body parts on verbal or nonverbal command	Body structure
Heterotopagnosia	Patients are unable to point to somebody else's body parts, while pointing to own body part is intact	Body structure
Macrosomatognosia	Perception of a body part as being larger than its actual size	Body (part) size
Microsomatognosia	Perception of a body part as being smaller than its actual size	Body (part) size
Hylognosia	An impairment in discriminating the microgeometrical features such as texture, density, or the thermal properties of an object	Haptic object recognition

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Table 3.1 (Continued)

Deficit	Description	Affected function
Morphognosia	An impairment in discriminating the macrogeometrical features such as size of shape of an object	Haptic object recognition
Tactile apraxia	Impairment in performing exploratory finger and hand movements during haptic object recognition. Basic motor and somatosensory function is intact	Haptic object recognition
Apperceptive tactile agnosia/ astereognosis	Impairment in building a coherent *representation* of the object based on the integration of the micro- and/or macrogeometrical properties	Haptic object recognition
Associative tactile agnosia	Deficit in recognizing object by touch when a representation of the object is achieved, but access to semantic knowledge about the object is lost, therefore blocking recognition	Haptic object recognition

objects placed on the arm compared to objects placed on the hand. The size of the objects placed on the hand were perceptually overestimated compared to objects placed on the forearm, consistent with Weber's illusion (Weber, 1834). However, when grasping the objects, maximum grip aperture was smaller for objects placed on the hand, showing the opposite pattern to the perceptual estimations. A recent study additionally used just notable difference scores to test whether manual size estimations and grasping movements toward the objects on the hand or forearm adhered to Weber's law (note this is not the same as Weber's illusion). Weber's law suggests that "just noticeable" is a constant ratio of the original stimulus magnitude and that the sensitivity of detecting a change in any physical continuum is relative as opposed to absolute. Thus, the just noticeable difference (JND) for smaller objects should be smaller than for larger objects (Davarpanah Jazi & Heath, 2014). Indeed, Davarpanah Jazi and Heath (2014) observed that grasping responses violated Weber's law, while the manual size estimates adhered to Weber's law, at least for objects on the hand. As such the study provided support for distinct processing of haptic size cues for perceptual estimates and for the guidance of action.

Another way to assess distinct processes for the perception and action is by using illusions. Indeed, the experience of our own body is highly malleable and several bodily illusions exist. One of the most widely known illusions is the rubber hand illusion (Botvinick & Cohen, 1998) (see Box 3.2). One way to assess the effect of the rubber hand illusion is

BOX 3.2 Bodily Illusions

We experience our body continuously and this experience appears to be veridical to us. However, just like with visual and auditory perception, bodily perception can be influenced by various illusions that reflect how sensory input is processed and also the influence of stored representations of our body. Perhaps the most well-known bodily illusion is the rubber hand illusion. This illusion, discovered at a Halloween party by Matthew Botvinick, is induced by stroking a visible rubber hand placed in front of the participant synchronously with the participants own hand that is hidden from view (Fig. 3.2) (Botvinick & Cohen, 1998). This results in the experience that the felt stroking actually occurs on the rubber hand and that the rubber hand is thus part of the participant's body.

Since its discovery, the rubber hand illusion has become a standard paradigm to investigate the feeling of body ownership experimentally. It has been used to study the necessary conditions for gaining body ownership over a foreign object. For example, it has been shown that the illusion can be induced entirely by using synchronized tactile input (Ehrsson, Holmes, & Passingham, 2005), but also when tactile input is anticipated but not experienced (Ferri, Chiarelli, Merla, Gallese, & Costantini, 2013). Moreover, it can also be induced using synchronized visuomotor input (Tsakiris, Prabhu, & Haggard, 2006). It can be local, only for the stimulated finger, but not for other fingers of the same hand (Tsakiris & Haggard, 2005). The foreign objects need to resemble to some extent a hand oriented toward the body (except when viewing in a mirror) (Tsakiris & Haggard, 2005), but skin color does not matter (Farmer, Tajadura-Jimenez, & Tsakiris, 2012). The type of tactile input also needs to match that of the observed touches (Ward et al., 2015).

Moreover, it has been used to assess body ownership deficits in various clinical populations. Patient groups that show a larger than normal rubber

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BOX 3.2 Bodily Illusions—cont'd

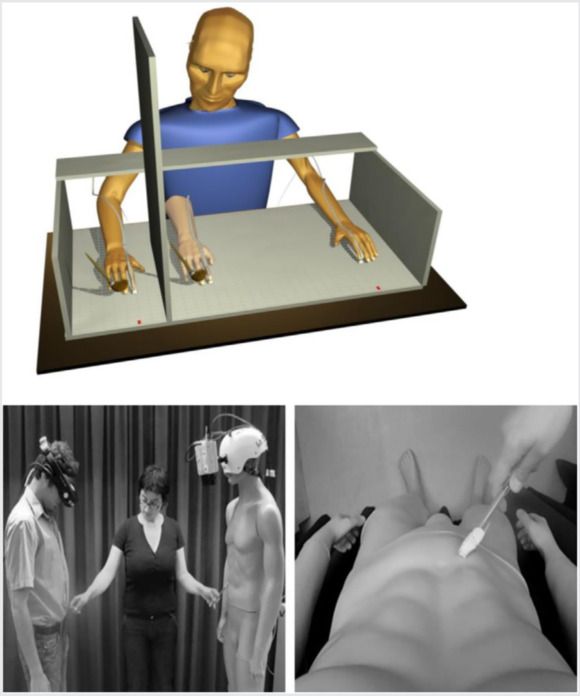

Figure 3.2 The rubber hand illusion and the full body illusion. *From Kammers, M. P. M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action.* Neuropsychologia *47(1), 204–211 and Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping.* PLoS One *3(12), e3832.*

hand illusion include patients with hemiplegia after stroke (for the paralyzed hand) (Burin et al., 2015), schizophrenic patients (Thakkar, Brugger, & Park, 2009), and anorexic individuals (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2014; Keizer, Smeets, Postma, van Elburg, & Dijkerman, 2014). A larger illusion has usually been linked to a reduced sense of ownership over their own body (part). Other clinical conditions are associated with a reduced rubber hand illusion. These include autistic individuals (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012) and also hemiplegic patients when the illusion is induced for their unaffected hand (Burin et al., 2015).

The rubber hand illusion has also inspired the development of other bodily illusions. These include the enfacement illusion in which participants watch a video of a face being stroked while simultaneously feeling face

(*Continued*)

BOX 3.2 Bodily Illusions—cont'd

stroking as well (Sforza, Bufalari, Haggard, & Aglioti, 2010), allowing them to experience ownership over the viewed face, but also a full body illusion (Petkova & Ehrsson, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). Here the participant views a different body from a first person's perspective through goggles (Fig. 3.2). The viewed body could be either a virtual body using virtual reality, or a mannequin or other person's body using a videolink to cameras attached to the other person's head. Again seeing the other body being stroked while simultaneously feeling the stroking on your own body results in the feeling that the other body belongs to you. A related illusion is the out of body illusion in which the participant views himself through a videolink from behind (Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Seeing your own body being stroked from the back and feeling it at the same time on your back results in the experience of being located behind your own body. Overall, these different illusions show that multisensory synchronized input is a powerful tool to modulate body ownership, at least if the viewed body (part) to some extent resembles the shape of the stimulated body (part).

Finally, other bodily illusions, that do not depend on synchronized multisensory input, exist as well. An example of such an illusion is the vibrotactile illusion in which a muscle tendon of, for example, the biceps muscle is vibrated at about 75 Hz. This creates an illusory extension of the arm (Kammers, van der Ham, & Dijkerman, 2006; Lackner, 1988). Interestingly, this experience can also affect a different body part (eg, a finger of the other hand) held by the stimulated arm (de Vignemont, Ehrsson, & Haggard, 2005; Lackner, 1988). This suggests that the vibrotactile illusion not only is an illusion based on peripheral sensory input but also affects higher order body representations.

to ask a participant to indicate *where* they feel their hand is (Botvinick & Cohen, 1998). In the illusion condition participants report the position of their hand to be shifted toward the rubber hand. However, this is only true for perceptual estimates, while reaching responses with or toward the illusion hand appear not to be influenced by the illusion (Kammers, Verhagen et al., 2009; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009). This finding is consistent with the idea that multiple body representations exist, which are activated based on the task at hand. A well-known distinction is that between the body image for perceptual experience of our body and body schema for the guidance of action (Gallagher, 2005; Paillard, 1999). This idea dates back to seminal work from Head and Holmes (Head & Holmes, 1911) who actually suggested three representations, a postural schema, a superficial tactile schema, and a body image. More recently, the concept of different body representations, and if so how many, has been hotly debated (de Vignemont, 2010; Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009). Indeed, there are several reports of bodily illusions influencing motor responses as well (Kammers, Kootker, Hogendoorn, & Dijkerman, 2009; Kammers, Longo et al., 2009; Newport, Pearce, & Preston, 2010), showing extensive interactions between somatosensory processing for perception and action. The challenge is to define the nature and specificity of the condition in which such interactions do and do not occur.

In the next section, we take a closer look at the characteristics of the spatial representations that underlie our bodily experience.

3.3 BODY SPACE

Many aspects of how we experience our body are spatial. We know where on our arm we feel an itch, what the position of our left hand is with respect to our right knee, etc. This bodily experience is multimodal in nature. We use input from our touch receptors in the skin, joint, and muscle receptors for proprioception, but also visual about the position of our body parts. Indeed, many of our bodily illusions (see Box 3.2) are induced by synchronized multisensory input about the body. Different spatial representations exist: a representation of our skin surface and a representation of our posture in joint coordinates are the most basic. However, higher order representation also exists. We have a template of the size and structure of body parts that influence our bodily perception as well. Each of these levels can also be distorted in patients with neurological of psychiatric deficits.

Here I review some of the processes that are involved in spatial processing pertaining to the body. Localizing a tactile stimulus on the body surface may be one of the most basic spatial body-related tasks we can perform. Yet, it involves a number of complex transformations (Longo, Azañón, & Haggard, 2010) (Fig. 3.3). A tactile stimulus is initially coded in somatotopic coordinates, for example, in a map of tactile receptors. However, there is no intrinsic link between this somatotopic representation and the body surface (Longo et al., 2010). For this a higher order representation is required, which according to Head and Holmes (1911) and Longo et al. (2010) would be the superficial schema. Deficits in linking somatotopic tactile input to a location on the body surface would result in

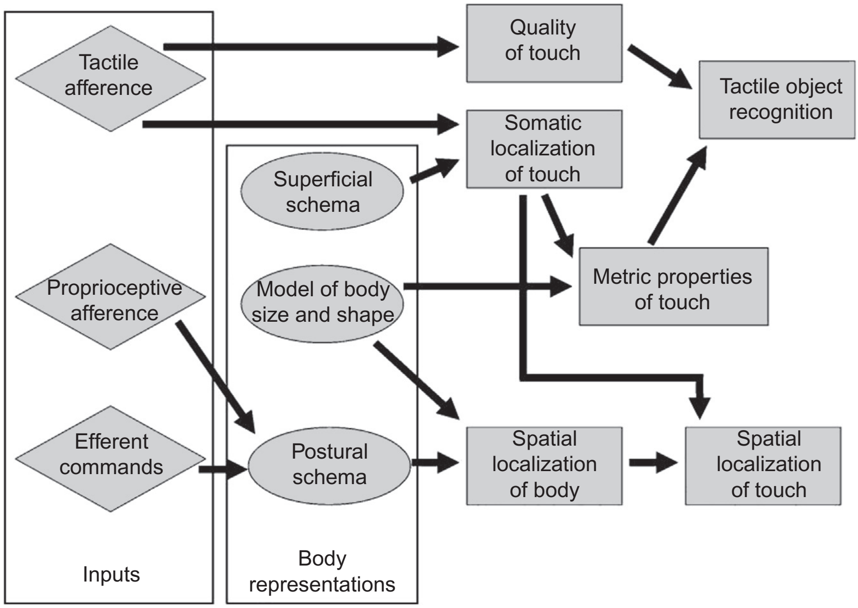

Figure 3.3 Different levels of somatosensory processing pertaining to the body. *From Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex.* Neuropsychologia *48(3), 655–668.*

patients being able to detect tactile stimuli, but making errors in localizing them. This type of deficit has been found in the earlier described study by Anema et al. (2009) and also by others (Halligan, Hunt, Marshall, & Wade, 1995).

Another aspect of body space is that we are able to localize where different body parts are with respect to each other and in external space. For this, proprioceptive input from receptors in joints, muscles, and tendons as well as tactile input about skin stretching is important. Efferent signals from the motor system may also play a role. However, while this input provides an estimate about the relative flexion or extension of body parts, it is not sufficient to localize body parts in external space (Longo et al., 2010). For this, information about the distance between joints, length and size of different body segments is needed. There are no afferent receptors that signal such features, therefore they must come from a stored representation, the postural schema (Head & Holmes, 1911; Longo et al., 2010). Thus, localizing body parts in external space would require a combination of afferent proprioceptive input and higher order stored representation. With respect to the neural correlate, evidence from neurophysiological as well as neuroimaging and patient studies suggest that particularly the posterior parietal cortex is involved in localizing body parts in external space (Graziano, Cooke, & Taylor, 2000; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006; Wolpert, Goodbody, & Husain, 1998).

Being able to localize a tactile stimulus in external space would subsequently require combining postural input about the position of body parts in external space with the localization of the tactile stimulus on the body surface (Longo et al., 2010). Studies in which tactile localization in external space is required using unusual postures shows that this process takes time. Yamamoto and Kitazawa (2001) used a temporal order judgment task for tactile stimuli given to the fingertips of the left and right hand while the arms were crossed or uncrossed. Participants were very accurate when the arms were uncrossed even for short interstimulus intervals. However, when the hands were crossed, a subgroup of the participants reversed the temporal order judgment when the two tactile stimuli were delivered within 300 ms from each other. They therefore responded as if the hands were not crossed coding the tactile stimuli in a body-centered somatotopic reference frame only. A similar finding was observed when recording saccades to tactile stimuli on crossed hands (Groh & Sparks, 1996). Interestingly, this remapping of tactile stimuli to external spatial reference frame may not be possible for fingers. The Aristotle illusion (Aristotle,1924) suggests that when crossing two fingers and touching with the inside of those two fingers an external object such as a pen or even your own nose, you feel two pens/noses. The explanation for this is that this posture is so unusual that the tactile input is processed as if the fingers are uncrossed. In a more experimental setting, it has been shown that temporal order and directional judgments of two successive tactile stimuli to adjacent crossed fingers are being performed as if the fingers were uncrossed, for example, in a somatotopic reference frame (de Haan, Anema, & Dijkerman, 2012; Heed, Backhaus, & Röder, 2011). Only, after experiencing a crossed finger posture for months does remapping occur (Benedetti, 1991). Furthermore, a patient with finger agnosia, the inability to recognize and distinguish between fingers did not show any problems with tactile localization in external space when crossing fingers (Anema, Overvliet, Smeets, Brenner, & Dijkerman, 2011), presumably because of an impaired prototypical finger representation (see also below structural representations). Another aspect that is important for localizing tactile stimuli in external space is the visual input. There is considerable evidence that visual experience is essential for remapping of tactile stimuli external space to occur. Röder, Rösler, and Spence (2004) showed that temporal order judgments of congenitally blind participants are *not* affected by crossing hands. In late blind these judgments are, however. This suggests that congenitally blind participants do not use an external reference frame for when localizing tactile stimuli. Interestingly, restoring sight in a congenitally blind individual at the age of two does not result in the use of external reference frame for localizing tactile stimuli, suggesting a sensitive period for remapping of tactile stimuli to develop (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013).

As mentioned before, peripheral somatosensory receptors do not provide information about the size of body parts (Longo et al., 2010). Nevertheless, we use body part size information when judging distances between two tactile stimuli on the body surface, or as described earlier when judging the position of body parts in external space.

Several studies suggest that visual input about the body is used to calibrate somatosensory size and distance perception. Differences in receptor density between body parts (Weinstein, 1968) results in a massively distorted somatotopic representation, with the hands and fingers being overrepresented compared, for example, to the arm and rump. This would create a problem for judgments of tactile size and distance, therefore, corrections need to be made. These corrections are based on visual information about the size of body parts (Taylor-Clarke, Jacobsen, & Haggard, 2004), however, these corrections are not perfect, resulting in minor differences in size or distance estimation depending on the stimulated body part (Weber, 1834). Thus the identical difference between two tactile stimuli is perceived as being larger for the hand (area with higher receptor density) than for the forearm (area with lower receptor density) (Weber's illusion).

Furthermore, we have an implicit representation of the size of different body parts that can be combined with tactile input for tactile size perception. This stored implicit body representation containing metric aspects of the body has been investigated in a series of studies by Longo and Haggard (2010). They asked participants to localize various landmarks of their unseen hand (eg, knuckles, fingertips) and used this localization to calculate distances between the landmarks. They argued that these distances provided information about the implicit body representation. Their results revealed a somewhat distorted implicit representation, with fingers being shorter than in reality and the width of the palm being wider. This characteristic may be related to the shape of the tactile receptive fields (Longo & Haggard, 2011). Similar distortions have also been reported for the entire body (overestimation of width, underestimation of length) (Fuentes, Longo, & Haggard, 2013). Other studies show that the characteristics of this implicit representation are indeed different from that of a visual-based explicit body image (Longo & Haggard, 2012).

Disturbances in body (part) size occur in various neurological and psychiatric conditions. Macrosomatognosia refers to the perception of a body part being larger than its actual size (Table 3.1). Patients with microsomatognosia experience their body (part) as being smaller (Frederiks, 1985). These deficits have been associated with a range of paroxysmal disorders such as migraine or seizures and often occur temporarily (Rode et al., 2012). They also have been reported for the affected hand in patients with complex regional pain syndrome (Peltz, Seifert, Lanz, Müller, & Maihöfner, 2011). Moreover, the perception of a smaller or larger body part can also be induced in healthy participants through proprioceptive illusions (de Vignemont et al., 2005) or through temporary peripheral proprioceptive deafferentation, which results in the affected body part feeling larger (Gandevia & Phegan, 1999). Damage to the central nervous also can affect body size perception. Macrosomatognosia is reported more frequently than microsomatognosia and is usually associated with parietal lesions (Frederiks, 1985). However, it has also been reported after a frontal lesion (Weijers, Rietveld, Meijer, & de Leeuw, 2013) or in Parkinson's patients (Sandyk, 1998).

The most well-known psychiatric condition in which body size distortions play a prominent role is anorexia nervosa. Indeed body image problems are a defining feature. Traditionally, investigations of body image disturbances have focused on visual body image and attitudinal aspects (Cash & Deagle, 1997; Farrell, Lee, & Shafran, 2005; Skrzypek, Wehmeier, & Remschmidt, 2001). However, more recent studies have investigated body size perception using input from other sensory modalities. Keizer and colleagues (Keizer et al., 2011; Keizer, Smeets, Dijkerman, van Elburg, & Postma, 2012) showed that anorexic participants overestimated the tactile distance between two stimuli, both on the forearm (a relatively neutral body part) and on the stomach (a sensitive body part). Moreover, anorexia patients also move as if their body is wider than in reality (Keizer et al., 2013). When walking through a door aperture, anorexia patient start rotating their shoulders for wider openings in relation to their shoulder width more than healthy participants do. This suggests that the body size distortion not only affects perceptual estimates, but also affects body size related action. Interestingly, body part size distortions appear to be reduced after inducing bodily illusions (Keizer, Smeets, Postma, van Elburg, & Dijkerman, 2014), suggesting that this distortion can be modulated.

While positional and size information about the body concerns more metric aspects of body space, other studies suggest the presence of structural representations. Structural body representation concerns the knowledge about the arrangement and form of body parts. Case studies of neurological patients with selective functional deficits reveal that such representations exist. One such impairment is autotopagnosia (Table 3.1). Patients are unable to point to their own body parts on verbal or nonverbal command (De Renzi, 1970; Sirigu, Grafman, Bressler, & Sunderland, 1991). Patients are able to name the body part and to describe its function (Guariglia, Piccardi, Allegra, & Traballesi, 2002; Sirigu et al., 1991), suggesting that semantic knowledge can be preserved (the opposite pattern has also been reported; Laiacona, Allamano, Lorenzi, & Capitani, 2006). Moreover, autotopagnosic patients can also point correctly to objects attached to the body parts (Sirigu et al., 1991), suggesting that sensorimotor function is intact as well (Buxbaum & Coslett, 2001). Impairments in body part matching across different orientations is also reported in these patients, suggesting that a structural description of the body is crucial (Buxbaum & Coslett, 2001). A related deficit is heterotopagnosia in which problems arise in pointing to somebody else's body parts when asked, while pointing to own body parts is intact (Auclair, Noulhiane, Raibaut, & Amarenco, 2009; Cleret de Langavant et al., 2012). Indeed, autotopagnosia and heterotopagnosia are double dissociated (Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003). Both disorders have been associated with left middle-temporal or parietal lesions of the dominant hemisphere (Schwoebel and Coslett, 2005), which is consistent with functional neuroimaging data of structural representations of the body (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008).

Structural body representation disorders not necessarily affect the whole body, but can selectively impair the fingers, or toes. In the case of "finger agnosia" patients are impaired when asked to identify the fingers despite a preserved ability to use them (Gerstman, 1940, Kinsbourne & Warrington, 1962) (Table 3.1). It usually affects the middle three fingers of both hands (Frederiks, 1985). Although finger agnosia was initially regarded as a form of autotopagnosia (Gerstmann, 1940), the disorders appeared to be dissociated (De Renzi and Scotti, 1970). Finger gnosis has been repeatedly associated with bilateral parietal activation (Rusconi, Walsh, & Butterworth, 2005). A recent study on the neuroanatomical correlates of finger gnosis specified that left anteromedial parietal lobule plays an important role in finger identification. (Rusconi et al., 2014). Finger agnosia can be considered to be a body image deficit, as tactile input to individual fingers can be used correctly to guide movements (Anema et al., 2008). Traditionally, finger agnosia was not regarded as a unitary phenomenon, but has been described as a part of a cluster of impairments, known as the Gerstmann's syndrome (Gerstmann, 1957). Gerstmann's syndrome is characterized by four core symptoms, that is, finger agnosia, dyscalculia, dysgraphia, and left–right disorientation. The latter is also regarded as a body representation disorder and concerns the impairment in the identification of the left and right side of one's own, and also someone else's body. Gerstmann's syndrome can also occur as a developmental disorder (Kinsbourne & Warrington, 1963).

The question remains however, whether Gerstmann's syndrome is a unitary disorder, or group of independent cognitive deficits that happen to co-occur relatively frequently, for example, due to white matter disconnection (Rusconi, Pinel, Dehaene, & Kleinschmidt, 2010) or whether other deficits should be included as well (Ardila, 2014).

3.4 ACTIVE TOUCH AND HAPTIC OBJECT RECOGNITION

In daily life we often use somatosensory information not only to inform us about our own body, but also to recognize objects in our environment. When switching off the alarm clock in the morning, which is situated next to a book, or when retrieving the keys from your pocket, which you need to distinguish from the wallet that is also in your pocket. Recognizing object by touch is not a passive process. We use active hand and finger movements to extract features about the to be recognized object. This is called haptic object recognition. The term haptic is used here to show that it involves more than just passive tactile input, but a combination of tactile and proprioceptive information gained through active exploratory hand movements. Different features are important: they include size, shape, weight, texture, and the hardness of the object. Haptic object features can be classified into two categories, concerning the micro- and macrogeometrical properties of an object (Morley, Goodwin, & Darian-Smith, 1983). Microgeometrical features pertain to texture, density, or thermal properties. They involve input from receptors in the skin of the observer. Size and shape are regarded as macrogeometrical properties. They are based on tactile as well as proprioceptive input from the muscle, tendon, and joint receptors. Evidence for segregation between micro- and macrogeometrical features comes from reports of selective impairments after brain damage. An impairment in discriminating the microgeometrical features such as texture, density, or the thermal properties of an object has been named hylognosia (Denes, 1989; Stralen & Dijkerman, 2011) (see also Table 3.1). Morphognosia is an impairment in the ability to discriminate the size or the shape of an object (macrogeometrical) (see also Table 3.1). Discriminating microgeometrical features of an object is associated with activation in the parietal operculum (Binkofski et al., 1999; O'Sullivan, Roland, & Kawashima, 1994; Roland, 1987). In contrast, processing of macrogeometrical properties is associated with the anterior part of the intraparietal sulcus, suggesting that these two different types of features are segregated at a neuroanatomical level (Caselli et al., 1991; Knecht et al., 1996; Hömke et al, 2009). The idea of two separate haptic feature processing disorders, however, is not undisputed. It has been argued that impairments in perceiving macrogeometrical properties of an object is a result of impaired spatial abilities. That is, perceiving the size or shape of an object requires an analysis of the direction and extension of the exploratory hand movement, the sense of limb position in space, and tactile localization (Saetti, De Renzi, & Comper, 1999). However, some patients with morphognosia showed no spatial deficits in other (visual) modalities (Reed, Caselli, & Farah, 1996).

As mentioned above, discrimination of features and recognizing an object haptically is not a passive process but requires exploratory hand and finger movements to gather information about the object. Seminal work by Lederman and Klatzky (Lederman & Klatzky, 1987, 1993) has shown that these exploratory hand movements are not random but directed for extracting the most relevant features. They described six exploratory procedures each aimed at extracting a specific object feature (Fig. 3.4). Thus, lateral motion is used to extract texture information, while unsupported holding can be used to get information about the object's weight (Lederman & Klatzky, 1993). Moreover, certain exploratory procedures, such as enclosure, provide information about more than one object feature and are relatively fast to perform. This exploratory procedure is therefore often the first choice when haptically trying to recognize an unknown object (Lederman & Klatzky, 1993). Interestingly,

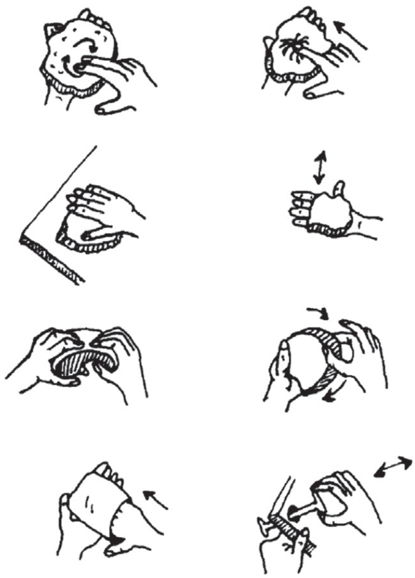

Figure 3.4 Different exploratory procedures for haptic object recognition. *From Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition.* Cognitive Psychology *19(3), 342–368.*

automatic techniques are now being developed to recognize different exploratory procedures, something which so far had to be done manually (Jansen, Bergmann Tiest, & Kappers, 2015).

Deficits in performing exploratory hand movement, while basic sensorimotor function is intact, are called "tactile apraxia" (see also Table 3.1), in which difficulties arise in adjusting hand movements to the characteristics of an object. Tactile apraxia is often linked to lesions in superior posterior parietal areas (Binkofski, Kunesch, Classen, Seitz, & Freund, 2001). Difficulties in the haptic exploration of an object can lead to problems in recognition of that object (Valenza et al., 2001), although this is not necessary (Caselli, 1991). Indeed, problems in object recognition can have different causes. Below, the haptic recognition of objects and their associated disorders are discussed, but first haptic perception of another spatial feature, orientation, is reviewed.

3.4.1 Haptic Processing of Orientation Information

Haptic perception of spatial features is not always veridical. Perhaps this is most evident for the processing of haptic spatial orientation. In a series of

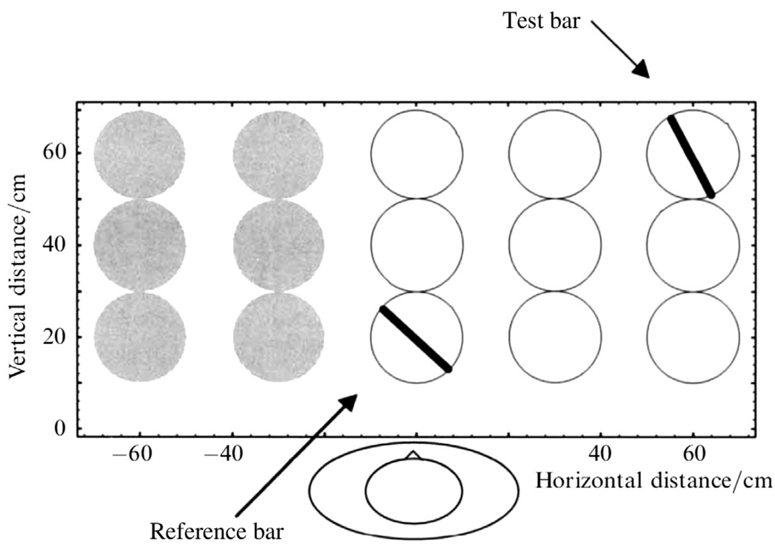

Figure 3.5 Setup of the parallel setting task. Blindfolded participants are required to haptically explore the reference bar and to rotate the test bar until both have the same orientation. *From Kappers, A. M., & Koenderink, J. J. (1999). Haptic perception of spatial relations.* Perception *28(6), 781–795.*

studies, Kappers and colleagues presented blindfolded participants with two metal bars that could rotate (Kappers & Koenderink, 1999). The reference bar was presented at one location in the workspace (Fig. 3.5), while the test bar was placed at a different location. Participants were asked to feel the orientation of the reference bar and to rotate the test bar until their orientations matched. Participants made large orientation errors (up to 40 degrees). These orientation errors depended on the horizontal distance between the two bars. Subsequent studies suggest that these errors appear to be a consequence of using hand-centered egocentric reference frames. That is, when judging the orientation of the bars participants relate it to the orientation of the hand with which the bar is felt. The orientation of the hand depends very much on where in the workspace the bar is positioned. When feeling a bar positioned on the right of the body midline, the hand is more in a clockwise orientation, while for bars on the left the hand is rotated anticlockwise. Interestingly, introducing a delay between presenting the reference bar and the test bar resulted in smaller errors, presumably because the participants started using a more allocentric reference frame for their responses (Zuidhoek, Kappers, Van Der Lubbe, & Postma, 2003). Similarly, when noninformative visual information is provided that allowed participants to favor coding in extrinsic coordinates it also resulted in improved performance (Newport, Rabb, & Jackson, 2002). Further corroborative evidence comes from a study with congenitally and late blind participants. Introducing a delay between the presentation of the reference and test bars resulted in an improvement in parallel setting for the late blind participants, but not for the congenitally blind participants (Postma, Zuidhoek, Noordzij, & Kappers, 2008). This suggests that visual experience is crucial for building the allocentric representation used during the delayed parallel setting task (see also chapter: On Inter and Intrahemispheric Differences in Visuospatial Perception).

3.4.2 Haptic Object Recognition

Besides intact somatosensory processing of features extracted using exploratory hand movements, recognizing objects by touch requires that multiple somatosensory signals are combined in a representation of an object. Information about the texture, shape, weight, and hardness needs to be gathered and integrated. Subsequently, semantic properties about the object (its use and function) are retrieved from memory. A deficit in building the object representation or in accessing the semantic properties results in "tactile agnosia" (Caselli, 1991; Denes, 1989; Endo, Miyasaka, Makishita, Yanagisawa, & Sugishita, 1992; Platz, 1996; Reed et al., 1996). In tactile agnosia, basic somatosensory processing is intact. Patients are also able to recognize objects through other sensory modalities. The problem in recognizing objects arises at higher levels. First, the problem could be one of building a coherent *representation* of the object based on the integration of the micro- and/or macrogeometrical properties. This is called tactile apperceptive agnosia or astereognosis (see also Table 3.1). These patients are unable to make an accurate drawing of the object they have explored haptically. Clinical reports of apperceptive agnosia without primary somatosensory or motor deficits are rare and are often linked to right hemispheric damage. Since the right hemisphere is associated with spatial perception, some authors have suggested that higher order tactile disorders are merely a consequence of impairments in spatial skills (Saetti et al., 1999; Semmes, 1965). Indeed, somatosensory impairments often occur together with deficits in higher order spatial processing such as hemispatial neglect (Vallar, 1997). However, other studies reported that tactile agnosia can exist without spatial deficits (Caselli, 1991; Reed et al., 1996).

Tactile associative agnosia is the second type of haptic object recognition deficit and occurs when a representation of an object is achieved (the patient can draw the haptically explored object), but access to semantic knowledge about the object is lost, therefore blocking recognition. Veronelli, Ginex, Dinacci, Cappa, and Corbo (2014) reported a case of pure associative agnosia of the left hand following a right hemorrhagic lesion limited to the post-central and supra-marginal gyri. This patient was unable to recognize objects only with the left hand, with a preserved tactile discrimination or visuotactile matching of objects. Indeed, patients with associative tactile agnosia can describe the object (eg, a soft round object in case of a ball) but are unable to indicate either the use or the name of the object. For this, semantic information from memory storage about this object is needed. Providing semantic cues about an object improves haptic recognition performance, suggesting that top-down mechanisms are involved in haptic processing (Bohlhalter, Fretz, & Weder, 2002).

3.5 PERIPERSONAL SPACE

It is now well-known that, in addition to body space, the area surrounding our body, in which objects are located that can be grasped or explored haptically, is represented separately as well. Peripersonal space representations are multimodal by nature, with visual (and also auditory) stimuli near a body part being coded together with tactile stimuli on that body part. Evidence for this idea comes from neurophysiological, neuropsychological, and behavioral studies.

Neurophysiological studies suggest that neurons in posterior parietal (area 7a, VIP) and (dorsal) premotor areas respond to tactile stimuli on the skin as well as to visual stimuli nearby (Bremmer, Schlack, Duhamel, Graf, & Fink, 2001; Duhamel, Colby, & Goldberg, 1998; Graziano & Cooke, 2006; Graziano et al., 2000; Rizzolatti, Luppino, & Matelli, 1998; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a) (Fig. 3.6). These bimodal neurons may show actual multimodal integration, in that they do respond in a nonlinear fashion when input from both modalities is present (Avillac, Ben Hamed, & Duhamel, 2007; Makin, Holmes, & Ehrsson, 2008). Their receptive fields have been found to be related mainly to the head and hand/arm and often code stimuli in body part-centered or head-centered coordinates (Bremmer et al., 2001) and, are sensitive to motion (approaching or moving away) (Bremmer et al., 2001; Duhamel et al., 1998) particularly to looming objects (Graziano & Cooke, 2006) and optic

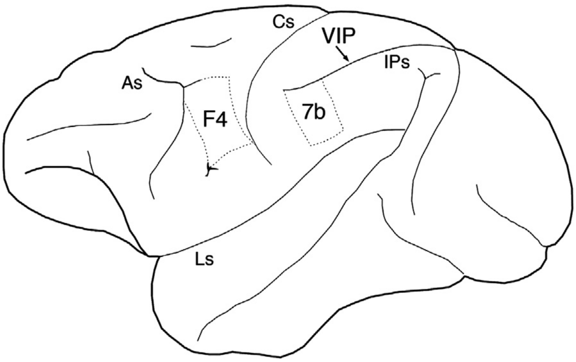

Figure 3.6 Cortical areas involved in multisensory coding of peripersonal space in the primate brain. *From di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain.* Neuropsychologia, *66, 126–133.*

flow during self-motion (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Graziano & Cooke, 2006). Moreover, they have been linked to a safety zone around the body and to defensive actions (Cooke and Graziano, 2004; Graziano, 2009; Graziano and Cooke, 2006). They respond to a realistic model of the hand and distinguish between the left and right arm (Graziano, 2000).

In humans, functional imaging reveals intraparietal sulcus and lateral occipital complex (LOC) activation for stimuli approaching the hand in near compared to far space (Makin, Holmes, & Zohary, 2007). In a more recent study, using a similar behavioral paradigm in combination with adaptation fMRI, Brozzoli also found involvement of anterior and inferior parietal regions when an object was approaching the hand in peripersonal space (Brozzoli, Gentile, Petkova, & Ehrsson, 2011). In addition, ventral and dorsal premotor adaptation was observed. Together these functional neuroimaging studies suggest that similar neural mechanisms coding a multimodal representation of peripersonal space may be present in humans as those reported based on neurophysiological studies in non-human primates.

In addition to the neurophysiological and neuroimaging findings reported above, there has been ample evidence for a visuotactile representation of peripersonal space from behavioral studies. In particular, cross-modal attentional cueing has shown that facilitation occurs when a visual cue near the hand is followed by a tactile stimulus on the hand (Driver and Spence, 1998; Spence, Lloyd, McGlone, Nicholls & Driver, 2000; Spence, Pavani, & Driver, 2000). This is the case for endogenous

(Eimer, van Velzen, & Driver, 2002; Spence, Pavani et al., 2000) as well as exogenous cues (Eimer and Driver, 2001; Kennett, Eimer, Spence, & Driver, 2001; Trenner et al., 2008). Similar effects have been reported for extinction after unilateral brain damage. These patients are impaired in detecting tactile stimuli on the contralesional side when accompanied by a visual stimulus on the ipsilesional side (Ladavas & Farne, 2004; Ladavas & Serino, 2008). Extinction is more pronounced when the visual stimulus is near the homologue body part on the ipsilesional side (Ladavas & Serino, 2008; Ladavas, di Pellegrino, Farne, & Zeloni, 1998). This is not the case when the visual stimulus was on the ipsilesional side far away from the body, nor when it was near a different part of the body (eg, face instead of hand) (Farne, Dematte, & Ladavas, 2005). Moreover, it moves with hand position (di Pellegrino, Ladavas, & Farne, 1997). Again, this suggests body part-centered coding, although other studies may suggest a more flexible coding in cross-modal extinction (Costantini, Bueti, Pazzaglia, & Aglioti, 2007; Tinazzi, Ferrari, Zampini, & Aglioti, 2000).

Recent studies suggest that a possible mechanism responsible for coding of peripersonal space may be visuotactile prediction (Clery, Guipponi, Odouard, Wardak, & Ben Hamed, 2015; Kandula, Hofman, & Dijkerman, 2014). That is, visual stimuli near the body are often followed by tactile stimuli on the body, therefore a tactile stimulus can automatically be anticipated following a nearby visual stimulus. Indeed, tactile processing is enhanced at the location and time predicted by an approaching visual stimulus (Clery et al., 2015; Gray & Tan, 2002; Kandula et al., 2014).

An important question is which function peripersonal spatial representation subserves. Several suggestions have been made, indeed prompting some research to suggest that different peripersonal space representations exist (De Vignemont & Iannetti, 2014). Originally peripersonal space was linked to preparation of motor acts (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981b). Indeed in more recent behavioral studies with human participants, peripersonal space has been linked to goal-directed sensorimotor responses (Brozzoli, Makin, Cardinali, Holmes, & Farne, 2012). Brozzoli et al. showed that visuotactile integration is also important when grasping toward neutral objects such as rectangular objects. They combined a cross-modal congruency task with visuomotor prehension and showed stronger congruency effects during the grasping movement than before (Brozzoli, Cardinali, Pavani, & Farne, 2010). Makin, Holmes, Brozzoli, and Farnè (2012) have suggested that bimodal hand-centered representations in particularly the premotor cortex are involved in rapid online control of action, following target perturbations. This contrasts to eye-centered coding of the target, which provides a more accurate representation of the object and hand position that may be used when more time is available.

As mentioned before, peripersonal space has also been considered as a safety zone around the body (see above) and thus has been linked to defensive actions. Graziano and colleagues reported that stimulation of the same neurones involved in visuotactile coding of peripersonal space evoke defensive actions like raising or withdrawing an arm (Graziano, 2009; Graziano & Cooke, 2006). In humans, responses to tactile stimuli seem to be enhanced when accompanied by threatening visual stimuli in peripersonal space such as spiders, snakes, or growling dogs (Poliakoff, Miles, Li, & Blanchette, 2007; Taffou & Viaud-Delmon, 2014; de Haan, Smit, Van der Stigchel, & Dijkerman, 2016).

Another aspect of peripersonal space coding that has received considerable attention recently is its social function. Various studies have provided direct evidence for the notion that visual social cues influence visuotactile representations of peripersonal space. Soto-Faraco assessed the role of visual social attention on tactile perception. They observed that eye gaze cued attention toward the location of a tactile target and resulted in improved perception at the cued location. This is consistent with the idea that attention is used to bias perceptual inference to optimize prediction (Soto-Faraco, Sinnett, Alsius, & Kingstone, 2005). A study by Heed, Habets, Sebanz, and Knoblich (2010) investigated visuotactile cross-modal congruency effects while another person was simultaneously performing a similar task. Cross-modal cueing effects were influenced by the partner, but only when he was situated near the participant and performed the same task. This suggests a direct link between social contextual factors and peripersonal space. A direct test of the effect of social cues on peripersonal space boundaries was performed by Teneggi et al. (2013). They used a recently developed method for determining peripersonal space boundary based on the effect of approaching auditory stimuli on tactile responses (Canzoneri, Magosso, & Serino, 2012) and tested whether the presence of a confederate standing nearby and facing the participant would affect this boundary. Their results showed that the peripersonal space boundary becomes smaller in such a situation. Follow-up experiments showed a merging of the peripersonal space of the two people during an economic game but only if they performed cooperatively. This suggests that peripersonal space boundaries can be modulated by the social context in which people interact. Another recent study by Maister, Cardini, Zamariola, Serino, and Tsakiris (2015) used a bodily illusion, the enfacement illusion, in which the participant and a confederate were touched simultaneously on the same cheek. The illusion induces a shared sensory experience between confederate and participant. Using the same audiotactile method to map peripersonal space boundary as Teneggi et al. (2013), Maister et al. (2015) showed that the participants were now also sensitive to audiotactile integration within the peripersonal space of the confederate. They further showed this did not happen in the space between the participant and the confederate. Thus, a remapping rather than an extension of peripersonal space had occurred. Overall, these studies show that social interactions modulate peripersonal space, however, some discrepancies remain with respect to the precise effects observed.

To summarize, a multimodal representation exists of the space surrounding our body, the peripersonal space. This representation has been found to be important for various functions, including defensive action, goal-directed visuomotor behavior, and social interactions. In the next section I will review the functional and neural mechanisms underlying one of these functions, visuomotor behavior.

3.6 VISUOMOTOR REACHING AND GRASPING

Spatial information required for goal-directed arm movements is provided by the visual as well as the somatosensory system. Both can provide input about the target toward which the hand moves as well as about the moving arm itself. Visual input about the target is processed in the posterior parietal areas along the visual dorsal stream (see also Chapter 2). Early neurophysiological single cell recordings in awake monkey have suggested that there are separate visuomotor channels for different types of visuomotor acts, for example, for reaching, grasping, saccadic, and smooth pursuit eye movements (Hyvärinen & Poranen, 1974; Milner & Dijkerman, 1998). Here we focus on hand and arm movements, as eye movements are discussed in Chapter 5. The distinct neural channels of visuomotor processing for reaching and grasping have been corroborated in more recent functional neuroimaging studies showing that grasping involves the human homologue of AIP, while reaching involves the superior parieto-occipital cortex (SPOC) (Gallivan, Cavina-Pratesi, & Culham, 2009). Indeed, several authors have suggested that reaching and grasping movements require different types of visual information. Reaching movements are dependent on spatial *location* data, while grasping movement involve nonspatial *size* input. Milner and Goodale (1995) argued that the involvement of the posterior parietal cortex in visually guided grasping is an important piece of evidence for the idea that the dorsal stream is not necessarily a spatial visual processing stream, but rather processes visual input for the guidance of action. Other evidence for the idea of separate visuomotor channels for reaching and grasping comes from studies of patients with optic ataxia (see also Chapter 3). Jeannerod, Decety, and Michel (1994) and Jakobson, Archibald, Carey, and Goodale (1991) described patients who had a selective visuomotor deficit for grasping, while reaching to specific locations appeared to be intact. fMRI studies also suggest that different routes within the visual dorsal stream are involved in reaching and grasping. Earlier neuroanatomical studies in monkeys suggested a distinction between dorsolateral and dorsomedial routes (Rizzolatti & Matelli, 2003). The dorsolateral route involved area the anterior part of the intraparietal sulcus (area AIP) (Fig. 3.7) projecting to the ventral portion of the premotor cortex. Based on neurophysiological studies, this route is considered to be involved in the sensory guidance of grasping movements. The dorsomedial route involves area V6A in monkeys or the superior parieto-occipital cortex in humans and is considered to process visual information for the guidance of reaching movements (Culham, Cavina-Pratesi, & Singhal, 2006; Rizzolatti & Matelli, 2003). However, the idea of separate visuomotor channels for reaching and grasping has been challenged based on evidence from different fields of study. First, recent neurophysiological studies suggest that the dorsolateral and dorsomedial routes have different functional properties than a distinction between reaching and grasping. Fattori, Breveglieri, Raos, Bosco, and Galletti (2012) observed grasping related activity in the dorsomedial area V6A. This is further substantiated by fMRI and combined EEG/TMS studies in humans (Verhagen et al., 2008, 2012). These studies suggest that both dorsolateral and dorsomedial routes are involved in visuomotor grasping but in a hierarchical manner. Area AIP within the dorsolateral route generates a fast motor plan based on available spatial and pictorial cues.

This information is then conveyed to the dorsomedial route which specifies motor parameters controlling arm, wrist, and finger movements with respect to object configuration just before movement onset (Verhagen et al., 2013).

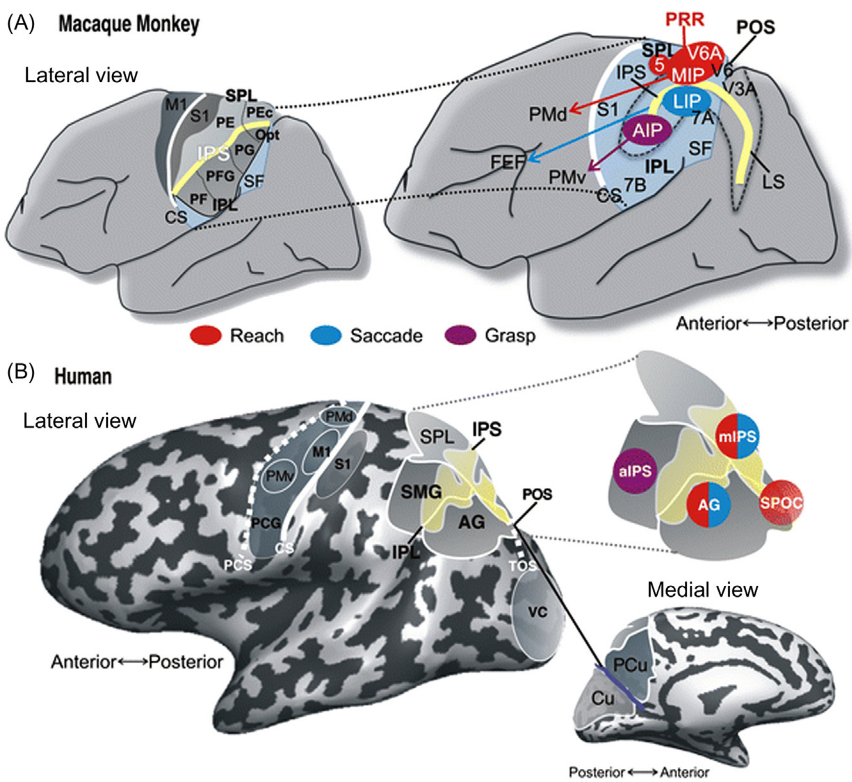

Figure 3.7 Posterior parietal areas involved in visuomotor control. *AIP*, Anterior part of the intraparietal sulcus (involved in grasping) and *MIP*, medial part of the intraparietal sulcus. *From Vesia, M., & Crawford, J. D. (2012). Specialization of reach function in human posterior parietal cortex.* Experimental Brain Research *221(1), 1–18.*

Other evidence against the idea of separate processing for reaching and grasping comes from behavioral studies. Smeets and Brenner (1999) suggested that grasping involves positioning the index finger and thumb on appropriate positions on the surface of the object, depending on characteristics such as object shape, fragility, reaching movement, and required accuracy. Grasping occurs by controlling index finger and thumb movements more or less independently and making sure that they approach the appropriate positions approximately orthogonal to the object surface. Thus, here grasping movements can be seen as two fingered pointing movements that also depend on spatial location data.

While grasping and reaching movements are both aimed toward an object in external space, in everyday behavior it is at least as important that we also avoid bumping into and knocking over objects that are in the way during a reaching/grasping movement. The next section reviews the literature on spatial processing during obstacle avoidance.

3.7 OBSTACLE AVOIDANCE

Two different types of processes have been considered to be relevant when grasping a target object when other objects are present. First, the nontarget object may act as a potential target. That is, the presence of the nontarget may induce competing motor responses toward these nontargets that need to be inhibited (see also chapter 5) (Howard & Tipper, 1997). This is based on the idea that in the posterior parietal cortex and in motor areas reach direction selective neurones exist that may be activated by stimuli in the environment. Any overlap between activations for target and nontarget leads to inhibition of the latter, resulting to reaching movements that deviate away from the nontargets. Indeed the presence of nontargets in the workspace leads to more activation in posterior parietal cortex in humans (Chapman et al., 2007). This deviation away can be observed even when the nontarget stimuli are not physical objects but, for example, LEDs. This is essentially a problem of *target selection*.

A second process that may be involved is that the visuomotor response is programmed in such a way as to avoid contact with the nontarget obstacle, for example, by maintaining a minimum distance (Tresilian, 1998). Evidence in line with this account comes from several studies reporting an increase in movement time when nontargets are present (Biegstraaten, Smeets, & Brenner, 2003; Jackson, Jackson, & Rosicky, 1995; Mon-Williams, Tresilian, Coppard, & Carson, 2001), suggesting that the grasping movement is slowed down to increase spatial accuracy and avoid potential collisions. These adjustments are not a general response to the presence of nontarget objects (Mon-Williams et al., 2001), on the contrary, the effect is specific to the layout of the workspace in that nontarget objects only elicit an avoidance response when the preferred distance to them is too small. Thus here obstacle avoidance is considered to be an aspect of action specification.

A more recent proposal combines both models and suggests that target selection and action specification run in parallel influencing each other and involving similar neural substrates in parietal and premotor areas (Cisek & Kalaska, 2010). It is therefore suggested that both are required and effects reported might not be uniquely attributable to either attentional allocation during target selection or movement planning.

Several features of the nontarget object appear to influence obstacle avoidance. First, evidently the position of the nontarget object is important. When the nontarget is closer to the path the hand would travel without obstacle larger deviations in the reaching trajectory occur. A recent study by Menger, Dijkerman, and Stigchel (2014) systematically varied nontarget positions during goal-directed grasping movements (Fig. 3.8). They observed various effects. First, objects on the outside of the reaching arm result in larger deviations, presumably because of the avoidance movement taking not only the hand, but also the attached arm trajectory into account (Menger, Van der Stigchel, & Dijkerman, 2012). Second, nontarget objects close to the starting position cause more deviation than those closer to the target object.

Importantly, it is not so much the absolute position of the nontarget obstacle that is relevant for programming an appropriate reaching response, but a combination of the distance and direction of this object, with the direction appearing to play a larger role. Other features of the nontarget object that appear to influence the grasping movement are

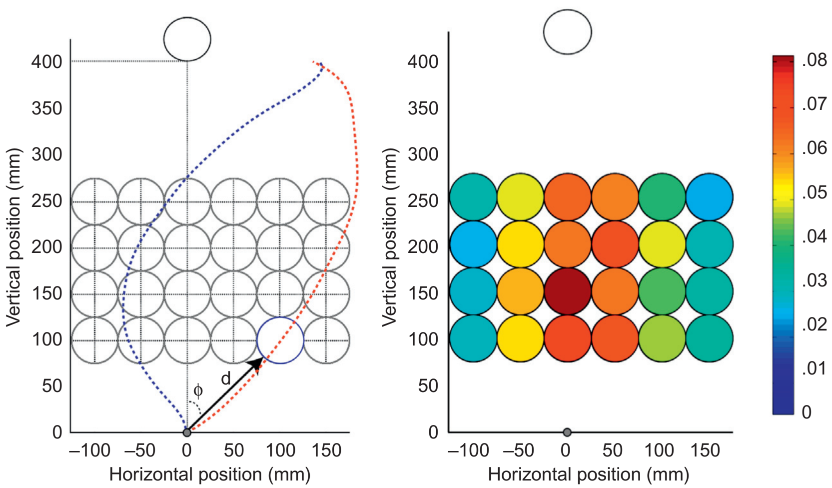

Figure 3.8 Effects of nontarget position on deviation of hand during reaching. Left: the layout of the different nontarget position (note only one nontarget was present in a particular trial) and example. Right: a schematic depiction of the amount of deviation (warmer colors mean more deviation). *From Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2014). On the relation between nontarget object location and avoidance responses.* Journal of Vision *14(9), 1–14.*

its size (height) and orientation (Alberts, Saling, & Stelmach, 2002; Chapman & Goodale, 2008; Saling, Alberts, Stelmach, & Bloedel, 1998). These features are all arguably processed by the visual dorsal stream. Indeed, patients suffering from optic ataxia following posterior parietal lesions are impaired in adjusting their reaching trajectory to the position of the nontarget objects (Schindler et al., 2004), while visual form agnosic patients with ventral stream lesions do adjust their reaching movements to the position of the obstacle (Rice et al., 2006). However, several authors have suggested that object identity should influence obstacle avoidance as well, as the consequences of a potential collision may influence the safety margin and these consequences can only be estimated when the identity of the obstacle is known. This idea was tested by de Haan, Van der Stigchel, Nijnens, and Dijkerman (2014). They asked participants to make reach-to-grasp movements while a glass was situated in the workspace. The glass could be empty or filled with water. Thus the spatial configuration of the obstacle was identical, while the possible consequences of collision with the obstacle differed. Indeed, the participants' reaching trajectories veered away more from the filled compared to the empty glass, showing that object recognition can influence avoidance behavior. However, even simpler nonspatial ventral stream related features can also influence reaching trajectories in an obstacle avoidance paradigm. Menger, Dijkerman, and Van der Stigchel (2013) showed that similarity in color between target and nontarget resulted in a larger deviation in reaching trajectory. This result is entirely consistent with the attentional target specification account of reaching trajectories in obstacle avoidance. Nevertheless, other studies (Menger et al., 2012) showed that nonattentional factors such as the posture of the reaching hand at the start of the movement also influence reaching trajectories, indicating that both target selection and movement specification are important, as suggested by Cisek and Kalaska (2010).

3.8 REFERENCE FRAMES IN VISUOMOTOR CONTROL

When reaching toward an object or when avoiding an obstacle while moving, it is important to know the location of the object with respect to the actor in order to program an accurate reaching movement. Indeed, it is widely acknowledged that sensory processing for the guidance of action occurs in egocentric coordinates. Milner and Goodale (1995) have suggested that the visuomotor dorsal stream processes visual information in entirely egocentric coordinates. In contrast, visual information processed in the ventral stream is essential for allocentric spatial representations, as identity information is required to tag individual items when localizing them with respect to each other (Milner, Dijkerman, & Carey, 1999). The well-studied visual form agnosic patient DF was demonstrated to have impaired allocentric coding, while egocentric coding remained intact (Carey, Dijkerman, Murphy, Goodale, & Milner, 2006; Dijkerman, Milner, & Carey, 1998; Schenk, 2006); however, allocentric categorical judgments were possible (Carey, Dijkerman, & Milner, 2009; see also Ruotolo, van der Ham, Postma, Ruggiero, & Iachini, 2015, Chapter 2). Similarly, introducing a delay between visual stimulus presentation and reaching response also results in healthy participants basing their reaching response on an allocentric rather than egocentric representation (Rossetti, 1998). As the visual dorsal stream is involved in the moment to moment calculation of the spatial position of the target, as target as well as observer tend to move around, introducing a delay presumably results in the use of ventral stream-based allocentric representations.

While it is clear that visuomotor responses depend on egocentric processing of items in the workspace, which type of egocentric representations is used has been a topic of much further investigation. The problem is that visual input about the stimulus is originally registered in retinotopic coordinates, while ultimately the reaching responses need to be computed in hand- or arm-centered coordinates. How does the brain solve this problem? Two different mechanisms have been proposed: First, using proprioceptive information about the position of the eye in the socket, retinotopic coordinates are transformed into head-centered coordinates. Adding proprioceptive input about the position of the head with respect to the trunk allows calculation of the position of the target with respect to the trunk. Finally proprioceptive input about the hand with respect to the trunk results in a hand-centered localization of the target object (Andersen, 1997). An alternative and more recent proposal is that that both target and effector (the hand) are localized in the same coordinate system. Indeed, there is considerable evidence that both hand and target are coded in eye-centered reference frames in the posterior parietal cortex.

Neurophysiological studies in monkeys show that targets and the hand are coding with respect to the eye (Batista, Buneo, Snyder, & Andersen, 1999; Buneo, Jarvis, Batista, & Andersen, 2002). Evidence for gaze-centered coding of reach targets in humans comes from patients with optic ataxia. These patients show errors when reaching for targets in their peripheral vision, while basic visual and motor function is intact. Several studies have shown that these reaching errors are linked to the direction of gaze, suggesting a gaze-centered coding of the target position (Dijkerman et al., 2006; Khan, Pisella, Rossetti, Vighetto, & Crawford, 2005; Khan, Pisella, Vighetto, et al., 2005). However, it is also clear that body- and hand-centered coding of targets exist as well. This has been shown using neurophysiology in monkeys (Buneo et al., 2002; Graziano & Gross, 1998; Hadjidimitrakis, Bertozzi, Breveglieri, Fattori, & Galletti, 2013). Neuroimaging studies with healthy participants also suggest that in the posterior parietal cortex and in the premotor cortex both gaze-centered coding and body part (hand)-centered coding exist (Beurze, Toni, Pisella, & Medendorp, 2010; Beurze, Van Pelt, & Medendorp, 2006). Transformation between the two reference frames may be achieved by vectorially subtracting hand location from target location which are both coded in eye-centered coordinates (Beurze et al., 2010; Buneo et al., 2002). Furthermore, reference frames may be used flexibly (Leoné, Henriques, Medendorp, & Toni, 2015), depending on the sensory context. That is, combined gaze- and body-centered reference frames may be used when reaching for visual targets, while for unseen proprioceptive targets body-centered reference frames may dominate (Bernier & Grafton, 2010).

The research on reference frames exemplifies the importance of both visual and somatosensory input during goal-directed movements. The next section discusses how visual and somatosensory input are combined.

3.9 HOW VISION AND SOMATOSENSORY INPUT ARE COMBINED DURING REACHING BEHAVIOR

Goal-directed movements inevitably require input from multiple sensory modalities. The most widely studied situation is where a visual target is shown toward which the participant moves. The somatosensory system then provides information about the location and configuration of the moving arm. Alternatively, information about the target location can be proprioceptive or tactile as well (see Section 3.2) and visual information about the moving hand can also be available.

Overall, there is considerable evidence to suggest that both the dorsolateral and the dorsomedial visual streams contain neurones involved in multimodal coding of body-related and arm-related configurations used for the guidance of action. For example, nonvisual neurones responding to somatosensory as well as bimodal stimulation have been found in primate area V6A (Breveglieri, Kutz, Fattori, Gamberini, & Galletti, 2002; Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003), which is part of the dorsomedial route. The same is true for area PEc, which lies just anterior to V6A (Breveglieri, Galletti, Monaco, & Fattori, 2008). Area AIP also responses to visual as well as somatosensory input. However, here it might be related more to tactile contact at the end of the grasping movement (Gardner et al., 2007; Grefkes, Weiss, Zilles, & Fink, 2002). Tactile input during contact with the target object at the end of grasping movements indeed is important for the absolute calibration between object features and the required motor output (Davarpanah, Hosang, & Heath, 2015; Heath & Holmes, 2015). Without tactile feedback the motor system relies on relative size cues to program hand opening during grasping. This is shown by studies with healthy participants in which removal of tactile feedback at the end of the movement changes the way maximum hand opening during the grasping movement relates to object width. Moreover, visual form agnosic patient DF, whose lesion affects ventral stream processing of size and shape cues, is highly dependent on tactile input at the end of the movement for normal grip scaling during goal-directed prehension movements (Schenk, 2012). This tactile input has been observed to be necessary to engage the visual dorsal stream (Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014).

Combining visual with somatosensory input can also be important when reaching for multisensory spatial targets. Traditionally, visual input is considered to provide more precise spatial information. Reaching errors to visual targets are often smaller than those to proprioceptive targets (von Hofsten & Rösblad, 1988). Indeed, proprioceptive localization tends to drift over time. Providing temporary visual input results in a reduction of this drift (Wann & Ibrahim, 1992). However, more recent studies show that differences in precision of localizing visual and proprioceptive targets depend on certain aspects of the task. First van Beers, Wolpert, and Haggard (2002) showed that proprioceptive target are localized more accurately than visual targets when they vary in depth. Second, when visual input is limited, proprioceptive input may increase precision of localization (Monaco et al., 2010). Overall, these findings are consistent with the idea that localization input is processed in statistically optimal integration from multiple modalities with the more reliably input receiving a higher weighting. This can even explain the patterns of proprioceptive drift and visual correction reported in the earlier experiment by

Wann & Ibrahim (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). This idea is similar to multimodal object perception (Ernst & Banks, 2002) (for more information about multisensory processes see also Chapter 4).

3.10 CONCLUSION

The aim of this chapter was to provide an overview of the spatial processes that are important for bodily experience and for sensory-guided action. Three different aspects were discussed in particular. First, spatial aspects of somatosensory processing were reviewed. Somatosensory input can provide information about external stimuli in the environment as well as about our own body. Both have been reviewed, including deficits in spatial aspects of somatosensory processing. A second topic has been the representation of the space surrounding our body, the peripersonal space. Final, the sensory processes, visual and nonvisual, that are important for reaching and grasping movements have been reviewed. The functional as well as neural organization underlying sensory-guided action was discussed. Although these three aspects are discussed separately, it is clear that they are interdependent. Thus reaching and grasping movements depend on somatosensory input about the spatial configuration of the hand and arm. Similarly, visuotactile representations of peripersonal space may be particularly relevant for reaching and grasping movements. And body representations such as the body schema have been linked to peripersonal space (Cardinali, Brozzoli, & Farne, 2009). This is also reflected in the underlying neural mechanisms, which mostly entail various frontoparietal networks for all three functions.

Furthermore, recent studies suggest that each of these three functions is also relevant for and influenced by other cognitive, social, and affective representations. Examples are the earlier mentioned social influences on peripersonal space boundaries, and also the role of body postures on emotion perception (de Gelder, 2006) and the link between body ownership and affective processing (van Stralen et al., 2014). Future research will no doubt further delineate the interactions between these different functions.

Final, for all these functions, neuropsychological studies of patients with selective deficits have been instrumental in delineating the neurocognitive architecture of these functions. This is true for visually guided actions (optic ataxia), body representation (eg, autotopagnosia), as well as peripersonal space (cross-modal extinction). These neuropsychological studies are invariably combined with evidence from other methodologies (neurophysiological, psychophysics, or neuroimaging). Nevertheless, neuropsychological studies have provided crucial evidence for functional models. I have no doubt this will continue to be the case.

REFERENCES

Alberts, J. L., Saling, M., & Stelmach, G. E. (2002). Alterations in transport path differentially affect temporal and spatial movement parameters. *Experimental Brain Research*, *143*(4), 417–425.

Andersen, R. A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *352*(1360), 1421–1428.

Anema, H. A., Overvliet, K. E., Smeets, J. B. J., Brenner, E., & Dijkerman, H. C. (2011). Integration of tactile input across fingers in a patient with finger agnosia. *Neuropsychologia*, *49*(1), 138–146.

Anema, H. A., van Zandvoort, M. J. E., de Haan, E. H. F., Kappelle, L. J., de Kort, P. L. M., Jansen, B. P. W., & Dijkerman, H. C. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia*, *47*(6), 1615–1620.

Anema, H. A., Wolswijk, V. W. J., Ruis, C., & Dijkerman, H. C. (2008). Grasping Weber's illusion: The effect of receptor density differences on grasping and matching. *Cognitive Neuropsychology*, *25*(7), 951–967.

Ardila, A. (2014). A proposed reinterpretation of Gerstmann's syndrome. *Archives of Clinical Neuropsychology*, *29*(November), 828–833.

Aristotle (1924). *Metaphysics (*W. D. Ross, Trans.*)*. Oxford: Oxford University Press.

Auclair, L., Noulhiane, M., Raibaut, P., & Amarenco, G. (2009). Where are your body parts? A pure case of heterotopagnosia following left parietal stroke. *Neurocase: Case Studies in Neuropsychology, Neuropsychiatry, and Behavioural Neurology*, *15*(6), 459–465.

Avillac, M., Ben Hamed, S., & Duhamel, J. R. (2007). Multisensory integration in the ventral intraparietal area of the macaque monkey. *The Journal of Neuroscience*, *27*(8), 1922–1932.

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science (New York, NY)*, *285*(5425), 257–260.

Benedetti, F. (1991). Perceptual learning following a long-lasting tactile reversal. *Journal of Experimental Psychology: Human Perception and Performance*, *17*(1), 267–277.

Bernier, P.-M., & Grafton, S. T. (2010). Human posterior parietal cortex flexibly determines reference frames for reaching based on sensory context. *Neuron*, *68*(4), 776–788.

Beurze, S. M., Toni, I., Pisella, L., & Medendorp, W. P. (2010). Reference frames for reach planning in human parietofrontal cortex. *Journal of Neurophysiology*, *104*(July 2010), 1736–1745.

Beurze, S. M., Van Pelt, S., & Medendorp, W. P. (2006). Behavioral reference frames for planning human reaching movements. *Journal of Neurophysiology*, *96*(1), 352–362.

Biegstraaten, M., Smeets, J. B. J., & Brenner, E. (2003). The influence of obstacles on the speed of grasping. *Experimental Brain Research*, *149*(4), 530–534.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research*, *128*(1–2), 210–213.

Binkofski, F., Kunesch, E., Classen, J., Seitz, R. J., & Freund, H. J. (2001). Tactile apraxia: Unimodal apractic disorder of tactile object exploration associated with parietal lobe lesions. *Brain*, *124*(Pt 1), 132–144.

Bjornsdotter, M., Loken, L., Olausson, H., Vallbo, Å., & Wessberg, J. (2009). Somatotopic organization of gentle touch processing in the posterior insular cortex. *The Journal of Neuroscience*, *29*(29), 9314–9320.

Bohlhalter, S., Fretz, C., & Weder, B. (2002). Hierarchical versus parallel processing in tactile object recognition: A behavioural-neuroanatomical study of aperceptive tactile agnosia. *Brain: A Journal of Neurology*, *125*(Pt 11), 2537–2548.

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see. *Nature*, *391* (6669), 756.

Bremmer, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2002). Heading encoding in the macaque ventral intraparietal area (VIP). *The European Journal of Neuroscience*, *16* (8), 1554–1568.

Bremmer, F., Schlack, A., Duhamel, J. R., Graf, W., & Fink, G. R. (2001). Space coding in primate posterior parietal cortex. *Neuroimage*, *14*(1 Pt 2), S46–S51.

Breveglieri, R., Galletti, C., Monaco, S., & Fattori, P. (2008). Visual, somatosensory, and bimodal activities in the macaque parietal area PEc. *Cerebral Cortex (New York, NY: 1991)*, *18*(4), 806–816.

Breveglieri, R., Kutz, D. F., Fattori, P., Gamberini, M., & Galletti, C. (2002). Somatosensory cells in the parieto-occipital area V6A of the macaque. *Neuroreport*, *13* (16), 2113–2116.

Brozzoli, C., Cardinali, L., Pavani, F., & Farne, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia*, *48*(3), 796–802.

Brozzoli, C., Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). FMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *The Journal of Neuroscience*, *31*(24), 9023–9031.

Brozzoli, C., Makin, T. R., Cardinali, L., Holmes, N., & Farne, A. (2012). Chapter 23 peripersonal space: A multisensory interface for body–object interactions. In M. Murray, & M. Wallace (Eds.), *The neural bases of multisensory processes* (pp. 1–13). Boca Raton, FL: CRC Press.

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632–636.

Burin, D., Livelli, A., Garbarini, F., Fossataro, C., Folegatti, A., Gindri, P., & Pia, L. (2015). Are movements necessary for the sense of body ownership? Evidence from the rubber hand illusion in pure hemiplegic patients. *PLoS One*, *10*(3), e0117155.

Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, *18*(4), 289–306.

Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS One*, *7*(9), e44306.

Cardinali, L., Brozzoli, C., & Farne, A. (2009). Peripersonal space and body schema: Two labels for the same concept? *Brain Topography*, *21*(3-4), 252–260.

Carey, D. P., Dijkerman, H. C., & Milner, A. D. (2009). Pointing to two imaginary targets at the same time: Bimanual allocentric and egocentric localization in visual form agnosic D.F. *Neuropsychologia*, *47*(6), 1469–1475.

Carey, D. P., Dijkerman, H. C., Murphy, K. J., Goodale, M. A., & Milner, A. D. (2006). Pointing to places and spaces in a patient with visual form agnosia. *Neuropsychologia*, *44*(9), 1584–1594.

Cascio, C. J., Foss-Feig, J. H., Burnette, C. P., Heacock, J. L., & Cosby, A. A. (2012). The rubber hand illusion in children with autism spectrum disorders: Delayed influence of combined tactile and visual input on proprioception. *Autism: The International Journal of Research and Practice*, *16*, 406–419.

Caselli, R. J. (1991). Rediscovering tactile agnosia. *Mayo Clinic Proceedings. Mayo Clinic*, *66*(2), 129–142.

Cash, T. F., & Deagle, E. A. (1997). The nature and extent of body-image disturbances in anorexia nervosa and bulimia nervosa: a meta-analysis. *The International Journal of Eating Disorders*, *22*(2), 107–125.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: The effect of obstacle position and size on avoidance while reaching. *Experimental Brain Research*, *191*(1), 83–97.

Chapman, H., Pierno, A. C., Cunnington, R., Gavrilescu, M., Egan, G., & Castiello, U. (2007). The neural basis of selection-for-action. *Neuroscience Letters*, *417*(2), 171–175.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, *33*(1), 269–298.

Cleret de Langavant, L., Trinkler, I., Remy, P., Thirioux, B., McIntyre, J., Berthoz, A., . . . Bachoud-Lévi, A.-C. (2012). Viewing another person's body as a target object: A behavioural and PET study of pointing. *Neuropsychologia*, *50*(8), 1801–1813.

Clery, J., Guipponi, O., Odouard, S., Wardak, C., & Ben Hamed, S. (2015). Impact prediction by looming visual stimuli enhances tactile detection. *Journal of Neuroscience*, *35* (10), 4179–4189.

Cooke, D. F., & Graziano, M. S. (2004). Sensorimotor integration in the precentral gyrus: Polysensory neurons and defensive movements. *Journal of Neurophysiology*, *91*(4), 1648–1660.

Corradi-Dell'Acqua, C., Hesse, M. D., Rumiati, R. I., & Fink, G. R. (2008). Where is a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. *Cerebral Cortex*, *18*(December), 2879–2890.

Costantini, M., Bueti, D., Pazzaglia, M., & Aglioti, S. M. (2007). Temporal dynamics of visuo-tactile extinction within and between hemispaces. *Neuropsychology*, *21*(2), 242–250.

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? *Neuropsychologia*, *44*(13), 2668–2684.

Davarpanah, S., Hosang, S., & Heath, M. (2015). Neuropsychologia memory delay and haptic feedback influence the dissociation of tactile cues for perception and action. *Neuropsychologia*, *71*, 91–100.

Davarpanah Jazi, S., & Heath, M. (2014). Weber's law in tactile grasping and manual estimation: Feedback-dependent evidence for functionally distinct processing streams. *Brain and Cognition*, *86*, 32–41.

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience*, 7(3), 242–249.

de Haan, A. M., Anema, H. A., & Dijkerman, H. C. (2012). Fingers crossed! An investigation of somatotopic representations using spatial directional judgements. *PLoS One*, 7(9), e45408.

de Haan, A. M., Van der Stigchel, S., Nijnens, C. M., & Dijkerman, H. C. (2014). The influence of object identity on obstacle avoidance reaching behaviour. *Acta Psychologica*, *150*, 94–99.

de Haan, A. M., Smit, M., Van der Stigchel, S., & Dijkerman, H. C. (2016). Approaching threat modulates visuotactile interactions in peripersonal space. *Experimental Brain Research*, . http://doi.org/10.1007/s00221-016-4571-2.

De Renzi, E., & Scotti, G. (1970). Autotopagnosia: Fiction or Reality? *Archives of Neurology*, *23*(3), 221.

de Vignemont, F. (2010). Body schema and body image—Pros and cons. *Neuropsychologia*, *48*(3), 669–680.

de Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology*, *15*(14), 1286–1290.

De Vignemont, F., & Iannetti, G. D. (2014). Neuropsychologia: How many peripersonal spaces? *Neuropsychologia*, 1–8.

Denes, G. (1989). Disorders of body awareness and body knowledge. In F. Boller, & J. Grafman (Eds.), *Handbook of neuropsychology* (pp. 207–225). Amsterdam: Elsevier Science Publishers.

di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia*, *66*, 126–133.

di Pellegrino, G., Ladavas, E., & Farne, A. (1997). Seeing where your hands are. *Nature*, *388*(6644), 730.

Dijkerman, H. C., & de Haan, E. H. (2007). Somatosensory processes subserving perception and action. *The Behavioral and Brain Sciences*, *30*(2), 139–189.

Dijkerman, H. C., McIntosh, R. D., Anema, H. A., de Haan, E. H. F., Kappelle, L. J., & Milner, A. D. (2006). Reaching errors in optic ataxia are linked to eye position rather than head or body position. *Neuropsychologia*, *44*(13), 2766–2773.

Dijkerman, H. C., Milner, A. D., & Carey, D. P. (1998). Grasping spatial relationships: Failure to demonstrate allocentric visual coding in a patient with visual form agnosia. *Consciousness and Cognition*, 7(3), 424–437.

Driver, J., & Spence, C. (1998). Crossmodal attention. *Current Opinion in Neurobiology*, *8* (2), 245–253.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neurophysiology*, *79*(1), 126–136.

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science (New York, NY)*, *317*(5841), 1048.

Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. *The Journal of Neuroscience*, *25*(45), 10564–10573.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science (New York, NY)*, *305* (5685), 875–877.

Eimer, M., & Driver, J. (2001). Crossmodal links in endogenous and exogenous spatial attention: Evidence from event-related brain potential studies. *Neuroscience and Biobehavioral Reviews*, *25*(6), 497–511.

Eimer, M., van Velzen, J., & Driver, J. (2002). Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *14*(2), 254–271.

Endo, K., Miyasaka, M., Makishita, H., Yanagisawa, N., & Sugishita, M. (1992). Tactile agnosia and tactile aphasia: Symptomatological and anatomical differences. *Cortex*, *28*(3), 445–469.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433.

Eshkevari, E., Rieger, E., Longo, M. R., Haggard, P., & Treasure, J. (2014). Persistent body image disturbance following recovery from eating disorders. *International Journal of Eating Disorders*, *47*, 400–409.

Farmer, H., Tajadura-Jiménez, A., & Tsakiris, M. (2012). Beyond the colour of my skin: How skin colour affects the sense of body-ownership. *Consciousness and Cognition*, *21* (3), 1242–1256.

Farne, A., Dematte, M. L., & Ladavas, E. (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology*, *65*(11), 1754–1758.

Farrell, C., Lee, M., & Shafran, R. (2005). Assessment of body size estimation: a review. *European Eating Disorders Review*, *13*, 75–88.

Fattori, P., Breveglieri, R., Raos, V., Bosco, A., & Galletti, C. (2012). Vision for action in the macaque medial posterior parietal cortex. *Journal of Neuroscience*, *32*(9), 3221–3234.

Felician, O., Ceccaldi, M., Didic, M., Thinus-Blanc, C., & Poncet, M. (2003). Pointing to body parts: A double dissociation study. *Neuropsychologia*, *41*(10), 1307–1316.

Ferri, F., Chiarelli, A. M., Merla, A., Gallese, V., & Costantini, M. (2013). The body beyond the body: Expectation of a sensory event is enough to induce ownership over a fake hand. *Proceedings. Biological Sciences/The Royal Society*, *280*(June), 20131140.

Frederiks, J. A. (1985). Macrosomatognosia and microsomatognosia. *Psychiatria, Neurologia, Neurochirurgia*, *66*, 531–536.

Fuentes, C. T., Longo, M. R., & Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica*, *144*(2), 344–351.

Gallagher, S. (2005). *How the body shapes the mind*. Oxford: Oxford University Press.

Galletti, C., Kutz, D. F., Gamberini, M., Breveglieri, R., & Fattori, P. (2003). Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. *Experimental Brain Research*, *153*(2), 158–170.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *The Journal of Neuroscience*, *29*(14), 4381–4391.

Gandevia, S. C., & Phegan, C. M. (1999). Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *The Journal of Physiology*, *514*(Pt 2), 609–616.

Gardner, E. P., Babu, K. S., Reitzen, S. D., Ghosh, S., Brown, A. S., Chen, J., ... Ro, J. Y. (2007). Neurophysiology of prehension. I. Posterior parietal cortex and object-oriented hand behaviors. *Journal of Neurophysiology*, *97*(1), 387–406.

Gerstmann, J. (1940). Syndrome of finger agnosia, disorientation for right and left, agraphia and aculculia. *Archives of Neurology and Psychiatry*, *44*, 398–407.

Gerstmann, J. (1957). Some notes on the Gerstmann syndrome. *Neurology*, 7(12), 866–869.

Gray, R., & Tan, H. Z. (2002). Dynamic and predictive links between touch and vision. *Experimental Brain Research*, *145*(1), 50–55.

Graziano, M. S. A. (2000). Coding the location of the arm by sight. *Science (New York, NY)*, *290*(5497), 1782–1786.

Graziano, M. S. (2009). *The intelligent movement machine*. New York: Oxford University Press.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845–859.

Graziano, M. S., & Gross, C. G. (1998). Spatial maps for the control of movement. *Current Opinion in Neurobiology*, *8*(2), 195–201.

Graziano, M. S., Cooke, D. F., & Taylor, C. S. (2000). Coding the location of the arm by sight. *Science (New York, NY)*, *290*(5497), 1782–1786.

Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: An fMRI study implies equivalencies between humans and monkeys. *Neuron*, *35*(1), 173–184.

Groh, J. M., & Sparks, D. L. (1996). Saccades to somatosensory targets. III. Eye-position-dependent somatosensory activity in primate superior colliculus. *Journal of Neurophysiology*, *75*(1), 439–453.

Guariglia, C., Piccardi, L., Allegra, M. C. P., & Traballesi, M. (2002). Is autotopoagnosia real? EC says yes: A case study. *Neuropsychologia*, *40*, 1744–1749.

Hadjidimitrakis, K., Bertozzi, F., Breveglieri, R., Fattori, P., & Galletti, C. (2013). Body-centered, mixed, but not hand-centered coding of visual targets in the medial posterior parietal cortex during reaches in 3D space. *Cerebral Cortex*, 1–12.

Halligan, P. W., Hunt, M., Marshall, J. C., & Wade, D. T. (1995). Sensory detection without localization. *Neurocase: Case Studies in Neuropsychology, Neuropsychiatry, and Behavioural Neurology, 1*, 259–266.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, *34*(2-3), 102–254.

Heath, M., & Holmes, S.A. (2015). An inverse grip starting posture gives rise to time-dependent adherence to Weber' s law: A reply to Ganel et al. (2014), *Journal of Vision*, *15*(6), 1–4.

Heed, T., Backhaus, J., & Röder, B. (2011). Integration of hand and finger location in external spatial coordinates for tactile localization. *Journal of Experimental Psychology: Human Perception and Performance*.

Heed, T., Habets, B., Sebanz, N., & Knoblich, G. (2010). Others' actions reduce cross-modal integration in peripersonal space. *Current Biology*, *20*(15), 1345–1349.

Hömke, L., Amunts, K., Bönig, L., Fretz, C., Binkofski, F., Zilles, K., & Weder, B. (2009). Analysis of lesions in patients with unilateral tactile agnosia using cytoarchitectonic probabilistic maps. *Human Brain Mapping*, *30*(5), 1444–1456.

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: Indirect evidence for inhibition. *Experimental Brain Research*, *113*, 144–152.

Hyvärinen, J., & Poranen, A. (1974). Function of parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain*, *97*, 673–692.

Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Experimental Brain Research*, *102*(3), 519–530.

Jakobson, L. S., Archibald, Y. M., Carey, D. P., & Goodale, M. A. (1991). A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia*, *29*, 803–809.

Jansen, S. E. M., Bergmann Tiest, W. M., & Kappers, A. M. L. (2015). Haptic exploratory behavior during object discrimination: A novel automatic annotation method. *PLoS One*, *10*(2), e0117017.

Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following posterior parietal lesion. *Neuropsychologia*, *32*, 369–380.

Kammers, M. P., Kootker, J. A., Hogendoorn, H., & Dijkerman, H. C. (2010). How many motoric body representations can we grasp? *Experimental Brain Research*, *202*(1), 203–212.

Kammers, M. P., Verhagen, L., Dijkerman, H. C., Hogendoorn, H., De Vignemont, F., & Schutter, D. J. (2009). Is this hand for real? Attenuation of the rubber hand illusion by transcranial magnetic stimulation over the inferior parietal lobule. *Journal of Cognitive Neuroscience*, *21*(7), 1311–1320.

Kammers, M. P. M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. *Neuropsychologia*, *47*(1), 204–211.

Kammers, M. P. M., Longo, M. R., Tsakiris, M., Dijkerman, H. C., & Haggard, P. (2009). Specificity and coherence of body representations. *Perception*, *38*(12), 1804–1820.

Kammers, M. P. M., van der Ham, I. J. M., & Dijkerman, H. C. (2006). Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia*, *44*(12), 2430–2436.

Kandula, M., Hofman, D., & Dijkerman, H. C. (2015). Visuo-tactile interactions are dependent on the predictive value of the visual stimulus. *Neuropsychologia*, *70*.

Kappers, A. M., & Koenderink, J. J. (1999). Haptic perception of spatial relations. *Perception*, *28*(6), 781–795.

Keizer, A., Smeets, M. A. M., Dijkerman, H. C., Uzunbajakau, S. A., van Elburg, A., & Postma, A. (2013). Too fat to fit through the door: First evidence for disturbed body-scaled action in anorexia nervosa during locomotion. *PLoS One*, *8*(5), e64602.

Keizer, A., Smeets, M. A. M., Dijkerman, H. C., van den Hout, M., Klugkist, I., van Elburg, A., & Postma, A. (2011). Tactile body image disturbance in anorexia nervosa. *Psychiatry Research*, *190*(1), 115–120.

Keizer, A., Smeets, M. A. M., Dijkerman, H. C., van Elburg, A., & Postma, A. (2012). Aberrant somatosensory perception in anorexia nervosa. *Psychiatry Research*, *200*(2–3), 530–537.

Keizer, A., Smeets, M. A. M., Postma, A., van Elburg, A., & Dijkerman, H. C. (2014). Does the experience of ownership over a rubber hand change body size perception in anorexia nervosa patients? *Neuropsychologia*, *62*, 26–37.

Kennett, S., Eimer, M., Spence, C., & Driver, J. (2001). Tactile-visual links in exogenous spatial attention under different postures: Convergent evidence from psychophysics and ERPs. *Journal of Cognitive Neuroscience*, *13*(4), 462–478.

Khan, A. Z., Pisella, L., Rossetti, Y., Vighetto, A., & Crawford, J. D. (2005). Impairment of gaze-centered updating of reach targets in bilateral parietal-occipital damaged patients. *Cerebral Cortex*, *15*(10), 1547–1560.

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., . . . Rossetti, Y. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience*, *8*(4), 418–420.

Kinsbourne, M., & Warrington, E. K. (1962). A study of finger agnosia. *Brain*, *85*, 47–66.

Kinsbourne, M., & Warrington, E. K. (1963). The developmental Gerstmann syndrome. *Archives of Neurology*, *8*, 490–501.

Knecht, S., Kunesch, E., & Schnitzler, A. (1996). Parallel and serial processing of haptic information in man: Effects of parietal lesions on sensorimotor hand function. *Neuropsychologia*, *37*, 669–687.

Klatzky, R. L., & Lederman, S. J. (1990). Intelligent exploration by the human hand. In V. Subramanian, & T. Iberall (Eds.), *Dextrous robot hands* (pp. 66–81). New York: Springer.

Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*, *111*(Pt 2), 281–297.

Ladavas, E., & Farne, A. (2004). Visuo-tactile representation of near-the-body space. *Journal of Physiology, Paris*, *98*(1-3), 161–170.

Ladavas, E., & Serino, A. (2008). Action-dependent plasticity in peripersonal space representations. *Cognitive Neuropsychology*, *25*(7-8), 1099–1113.

Ladavas, E., di Pellegrino, G., Farne, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, *10*(5), 581–589.

Laiacona, M., Allamano, N., Lorenzi, L., & Capitani, E. (2006). A case of impaired naming and knowledge of body parts. Are limbs a separate sub-category? *Neurocase: Case Studies in Neuropsychology, Neuropsychiatry, and Behavioural Neurology*, *12*(5), 307–316.

Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition. *Cognitive Psychology*, *19*(3), 342–368.

Lederman, S. J., & Klatzky, R. L. (1993). Extracting object properties through haptic exploration. *Acta Psychologica*, *84*(1), 29–40.

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science (New York, NY)*, *317*(5841), 1096–1099.

Leoné, F. T. M., Henriques, D. Y. P., Medendorp, W. P., & Toni, I. (2015). Flexible reference frames for grasp planning in human parietofrontal cortex. *Cortex, Human Parietofrontal*, *2*(June), 1–15.

Ley, P., Bottari, D., Shenoy, B. H., Kekunnaya, R., & Röder, B. (2013). Partial recovery of visual–spatial remapping of touch after restoring vision in a congenitally blind man. *Neuropsychologia*, *51*(6), 1119–1123.

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 11727–11732.

Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(3), 720–726.

Longo, M. R., & Haggard, P. (2012). Implicit body representations and the conscious body image. *Acta Psychologica*, *141*(2), 164–168.

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, *48*(3), 655–668.

Maister, L., Cardini, F., Zamariola, G., Serino, A., & Tsakiris, M. (2015). Your place or mine: Shared sensory experiences elicit a remapping of peripersonal space. *Neuropsychologia*, *70*, 455–461.

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, *191*(1), 1–10.

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *The Journal of Neuroscience*, *27*(4), 731–740.

Makin, T. R., Holmes, N. P., Brozzoli, C., & Farnè, A. (2012). Keeping the world at hand: Rapid visuomotor processing for hand-object interactions. *Experimental Brain Research*, *219*(4), 421–428.

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2013). The effect of similarity: Non-spatial features modulate obstacle avoidance. *PLoS One*, *8*(4), e59294.

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2014). On the relation between nontarget object location and avoidance responses. *Journal of Vision*, *14*(9), 1–14.

Menger, R., Van der Stigchel, S., & Dijkerman, H. C. (2012). How obstructing is an obstacle? The influence of starting posture on obstacle avoidance. *Acta Psychologica*, *141*(1), 1–8.

Milner, A. D., & Dijkerman, H. C. (1998). Visual processing in the primate parietal lobe. In A. D. Milner (Ed.), *Comparative neuropsychology* (pp. 70–94). Oxford: Oxford University Press.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785.

Milner, A. D., Dijkerman, H. C., & Carey, D. P. (1999). Visuospatial processing in a pure case of visual-form agnosia. In N. Burgess, K. J. Jeffery, & J. O. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition* (pp. 443–466). Oxford: Oxford University Press.

Monaco, S., Króliczak, G., Quinlan, D. J., Fattori, P., Galletti, C., Goodale, M. A., & Culham, J. C. (2010). Contribution of visual and proprioceptive information to the precision of reaching movements. *Experimental Brain Research*, *202*(1), 15–32.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Experimental Brain Research*, *137*(3-4), 497–501.

Morley, J. W., Goodwin, A. W., & Darian-Smith, I. (1983). Tactile discrimination of gratings. *Experimental Brain Research*, *49*(2), 291–299.

Moseley, G. L., Gallace, A., & Spence, C. (2012). Bodily illusions in health and disease: Physiological and clinical perspectives and the concept of a cortical "body matrix". *Neuroscience and Biobehavioral Reviews*, *36*(1), 34–46.

Newport, R., Pearce, R., & Preston, C. (2010). Fake hands in action: Embodiment and control of supernumerary limbs. *Experimental Brain Research*, *204*(3), 385–395.

Newport, R., Rabb, B., & Jackson, S. R. (2002). Noninformative vision improves haptic spatial perception. *Current Biology: CB*, *12*(19), 1661–1664.

O'Sullivan, B. T., Roland, P. E., & Kawashima, R. (1994). A PET study of somatosensory discrimination in man. *Microgeometry Versus Macrogeometry*, *6*, 137–148.

Paillard, J. (1999). Body schema and body image—A double dissociation in deafferented patients. In G.N. Gantchev, S. Mori, & J. Massion (Eds.), *Motor control, today and tomorrow* (pp. 198–214). Sofia: Academic Publishing House.

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content. A tactile analogue of "blind sight". *Archives of Neurology*, *40*(9), 548–551.

Pellijeff, A., Bonilha, L., Morgan, P. S., McKenzie, K., & Jackson, S. R. (2006). Parietal updating of limb posture: An event-related fMRI study. *Neuropsychologia*, *44*(13), 2685–2690.

Peltz, E., Seifert, F., Lanz, S., Müller, R., & Maihöfner, C. (2011). Impaired hand size estimation in CRPS. *The Journal of Pain*, *12*(10), 1095–1101.

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS One*, *3*(12), e3832.

Platz, T. (1996). Tactile agnosia. Casuistic evidence and theoretical remarks on modality-specific meaning representations and sensorimotor integration. *Brain*, *119*(Pt 5), 1565–1574.

Poliakoff, E., Miles, E., Li, X., & Blanchette, I. (2007). The effect of visual threat on spatial attention to touch. *Cognition*, *102*(3), 405–414.

Postma, A., Zuidhoek, S., Noordzij, M. L., & Kappers, A. M. L. (2008). Haptic orientation perception benefits from visual experience: Evidence from early-blind, late-blind, and sighted people. *Perception & Psychophysics*, *70*(7), 1197–1206.

Reed, C. L., Caselli, R. J., & Farah, M. J. (1996). Tactile agnosia: Underlying impairment and implications for normal tactile object recognition. *Brain*, *119*, 875–888.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Experimental Brain Research*, *174*(1), 176–188.

Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, *153*(2), 146–157.

Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: New concepts. *Electroencephalography and Clinical Neurophysiology*, *106*(4), 283–296.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981a). Afferent properties of periarcuate neurons in macaque monkeys. I. Somatosensory responses. *Behavioural Brain Research*, *2*(2), 125–146.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981b). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behavioural Brain Research*, *2*(2), 147–163.

Rode, G., Vallar, G., Revol, P., Tilikete, C., Jacquin-Courtois, S., Rossetti, Y., & Farne, A. (2012). Facial macrosomatognosia and pain in a case of Wallenberg's syndrome: Selective effects of vestibular and transcutaneous stimulations. *Neuropsychologia*, *50*(2), 245–253.

Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Current Biology*, *14*, 121–124.

Roland, P. E. (1987). Somatosensory detection of microgeometry, macrogeometry and kinesthesia after localized lesions of cerebral hemispheres in man. *Brain Research Reviews*, *12*, 43–94.

Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness and Cognition*, *7*, 520–558.

Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaethetic information: A dissociation between where and how. *Neuroreport*, *6*, 506–510.

Ruotolo, F., van der Ham, I., Postma, A., Ruggiero, G., & Iachini, T. (2015). How coordinate and categorical spatial relations combine with egocentric and allocentric reference frames in a motor task: Effects of delay and stimuli characteristics. *Behavioural Brain Research*, *284*, 1−12.

Rusconi, E., Pinel, P., Dehaene, S., & Kleinschmidt, A. (2010). The enigma of Gerstmann's syndrome revisited: A telling tale of the vicissitudes of neuropsychology. *Brain: A Journal of Neurology*, *133*(Pt 2), 320−332.

Rusconi, E., Walsh, V., & Butterworth, B. (2005). Dexterity with numbers: rTMS over left angular gyrus disrupts finger gnosis and number processing. *Neuropsychologia*, *43* (11), 1609−1624.

Saetti, M. C., De Renzi, E., & Comper, M. (1999). Tactile morphagnosia secondary to spatial deficits. *Neuropsychologia*, *37*(9), 1087−1100.

Saling, M., Alberts, J., Stelmach, G. E., & Bloedel, J. R. (1998). Reach-to-grasp movements during obstacle avoidance. *Experimental Brain Research*, *118*(2), 251−258.

Sandyk, R. (1998). Reversal of a body image disorder (macrosomatognosia) in Parkinson's disease by treatment with AC pulsed electromagnetic fields. *International Journal of Neuroscience*, *93*(1-2), 43−54.

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nature Neuroscience*, *9*(11), 1369−1370.

Schenk, T. (2012). No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *The Journal of Neuroscience*, *32*(6), 2013−2017.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: Evidence from optic ataxia. *Nature Neuroscience*, *7*(7), 779−784.

Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *J Cogn Neurosci*, *17*(4), 543−553.

Semmes, J. (1965). A non-tactual factor in astereognosis. *Neuropsychologia*, *3*, 295−315.

Sforza, A., Bufalari, I., Haggard, P., & Aglioti, S. M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Social Neuroscience*, *5*(October 2014), 148−162.

Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain*, *114*, 629−642.

Skrzypek, S., Wehmeier, P. M., & Remschmidt, H. (2001). Body image assessment using body size estimation in recent studies on anorexia nervosa. A brief review. *European Child & Adolescent Psychiatry*, *10*(4), 215−221.

Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS One*, *5*(5), e10564.

Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, *3*(3), 237−271.

Smeets, J. B. J., van den Dobbelsteen, J. J., de Grave, D. D. J., van Beers, R. J., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(49), 18781−18786.

Soto-Faraco, S., Sinnett, S., Alsius, A., & Kingstone, A. (2005). Spatial orienting of tactile attention induced by social cues. *Psychonomic Bulletin & Review*, *12*(6), 1024−1031.

Spence, C., Lloyd, D., McGlone, F., Nicholls, M. E., & Driver, J. (2000). Inhibition of return is supramodal: A demonstration between all possible pairings of vision, touch, and audition. *Experimental Brain Research*, *134*(1), 42−48.

Spence, C., Pavani, F., & Driver, J. (2000). Crossmodal links between vision and touch in covert endogenous spatial attention. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(4), 1298−1319.

Taffou, M., & Viaud-Delmon, I. (2014). Cynophobic fear adaptively extends peripersonal space. *Frontiers in Psychiatry*, *5*(September), 3–9.

Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, *7*(3), 219–220.

Teneggi, C., Canzoneri, E., Pellegrino, G., Serino, A., Giuridiche, S., Cicu, A., . . . Paris, I. (2013). Report social modulation of peripersonal space boundaries. *Current Biology*, *23*(5), 406–411.

Thakkar, K. N., Brugger, P., & Park, S. (2009). Exploring empathic space: Correlates of perspective transformation ability and biases in spatial attention. *PLoS One*, *4*(6), e5864.

Tinazzi, M., Ferrari, G., Zampini, M., & Aglioti, S. M. (2000). Neuropsychological evidence that somatic stimuli are spatially coded according to multiple frames of reference in a stroke patient with tactile extinction. *Neuroscience Letters*, *287*(2), 133–136.

Trenner, M. U., Heekeren, H. R., Bauer, M., Rossner, K., Wenzel, R., Villringer, A., & Fahle, M. (2008). What happens in between? Human oscillatory brain activity related to crossmodal spatial cueing. *PLoS One*, *3*(1), e1467.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Experimental Brain Research*, *120*(3), 352–368.

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(1), 80–91.

Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, *15*(2), 423–432.

Valenza, N., Ptak, R., Zimine, I., Badan, M., Lazeyras, F., & Schnider, A. (2001). Dissociated active and passive tactile shape recognition: A case study of pure tactile apraxia. *Brain*, *124*(Pt 11), 2287–2298.

Vallar, G. (1997). Spatial frames of reference and somatosensory processing: A neuropsychological perspective. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *352*(1360), 1401–1409.

van Beers, R. J., Wolpert, D. M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, *12*(10), 834–837.

van Stralen, H. E., & Dijkerman, H. C. (2011). Central touch disorders. *Scholarpedia*, *6*(10), 8243.

van Stralen, H. E., van Zandvoort, M. J. E., Vissers, L. M. G., Hoppenbrouwers, S. S., Kappelle, L. J., & Dijkerman, H. C. (2014). Affective touch modulates the rubber hand illusion. *Cognition*, *131* (1), 147–158.

Verhagen, L., Dijkerman, H. C., Grol, M. J., & Toni, I. (2008). Perceptuo-motor interactions during prehension movements. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(18), 4726–4735.

Verhagen, L., Dijkerman, H. C., Medendorp, W. P., & Toni, I. (2012). Cortical dynamics of sensorimotor integration during grasp planning. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(13), 4508–4519.

Verhagen, L., Dijkerman, H. C., Medendorp, W. P., & Toni, I. (2013). Hierarchical organization of parietofrontal circuits during goal-directed action. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *33*(15), 6492–6503.

Veronelli, L., Ginex, V., Dinacci, D., Cappa, S. F., & Corbo, M. (2014). Pure associative tactile agnosia for the left hand: Clinical and anatomo-functional correlations. *Cortex*, *58*, 206–216.

Vesia, M., & Crawford, J. D. (2012). Specialization of reach function in human posterior parietal cortex. *Experimental Brain Research*, *221*(1), 1–18.

von Hofsten, C., & Rösblad, B. (1988). The integration of sensory information in the development of precise manual pointing. *Neuropsychologia*, *26*(6), 805–821.

Wann, J. P., & Ibrahim, S. F. (1992). Does limb proprioception drift? *Experimental Brain Research*, *91*(1), 162–166.

Ward, J., Mensah, A., Jünemann, K., Ward, J., Mensah, A., & Jünemann, K. (2015). The rubber hand illusion depends on the tactile congruency of the observed and felt touch. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(5), 1203–1208.

Weber, E. H. (1834). In H. E. Ross, & D. J. Murray (Eds.), *The sense of touch*. London: Academic.

Weijers, N. R., Rietveld, A., Meijer, F. J. A., & de Leeuw, F. E. (2013). Macrosomatognosia in frontal lobe infarct-a case report. *Journal of Neurology*, *260*(3), 925–926.

Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In D. R. Kenskalo (Ed.), *The skin senses* (pp. 195–222). Sprinfield, IL: Charles C. Thomas.

Westwood, D. A., & Goodale, M. A. (2003). A haptic size-contrast illusion affects size perception but not grasping. *Experimental Brain Research*, *153*, 253–259.

Whitwell, R. L., David Milner, A., Cavina-Pratesi, C., Byrne, C. M., & Goodale, M. A. (2014). DF's visual brain in action: The role of tactile cues. *Neuropsychologia*, *55*, 41–50.

Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations: The role of the human superior parietal lobe. *Nature Neuroscience*, *1*(6), 529–533.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, *4*(7), 759–765.

Zuidhoek, S., Kappers, A. M., Van Der Lubbe, R. H., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research*, *149*(3), 320–330.