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**VISUAL-SOMATOSENSORY INTERACTIONS IN MENTAL
REPRESENTATIONS OF THE BODY AND THE FACE**

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Abstract

The body is represented in the brain at multiple levels. Some of these representational levels incorporate information from more than one of the senses, thus allowing information about the body from one sensory modality to influence the processing of body-related input to another. The experiments in this thesis focused on interactions between vision and cutaneous sensations (i.e., touch and pain), and what these interactions can tell us about mental representations of the body and the face. Experiment 1 revealed that there are at least partially dissociable pathways for visual enhancement of touch (VET) depending upon whether one sees one's own body or the body of another person. This indicates that VET, a seeming low-level effect of viewing the body on spatial tactile acuity, is actually sensitive to body identity. Experiments 2, 3, and 4 explored the effect of viewing one's own body on pain perception. They demonstrated that viewing the body can have at least two distinct effects. First, it can bias pain intensity judgments irrespective of the actual stimulus intensity. Second, and more importantly, it reduces the discriminative capacities of the nociceptive pathway encoding noxious stimulus intensity, but only if the pain-inducing event itself is not visible. This latter finding suggests that viewing the body alone and viewing a stimulus event on the body may have distinct effects on cutaneous sensations. The effect of viewing the body being touched was explored further in Experiment 5, which replicated previous findings that 1) viewing another person's face being touched improves detection of near-threshold tactile stimuli, and 2) this visual remapping of touch (VRT) is enhanced if the other person's face has a fearful expression. Experiment 5 also extended these previous findings by demonstrating that VRT does not occur for observed touch on non-human faces, even fearful ones. This suggests that the facial expressions of non-human animals may not be simulated within the somatosensory system of the human observer in the same way that the facial expressions of other humans are. Finally, Experiment 6 examined the enfacement illusion, in which seeing another person's face being

touched in synchrony with touch on one's own face causes the other's face to be assimilated into the mental self-face representation. Interestingly, the strength of the enfacement illusion was not affected if the other person showed a fearful or an angry facial expression, supporting the existence of an asymmetric relationship between the analyses of facial identity and facial expressions. Together, these studies indicate that multisensory representations of the body in the brain link low-level perceptual processes with the perception of emotional cues and body/face identity, and interact in complex ways depending upon contextual factors.

Introduction

I. Multiple representations of the body

While many avenues of research in cognitive neuroscience focus, understandably, on the brain itself, the sensory and motor capacities of this special organ would be ineffective without its linkages to the rest of the body. The body is the interface through which the brain learns about and effects change on its environment. Consequently, sensory and motor representations of the body are fundamental to brain function. What is more, the sense of the body as a coherent, unified entity acting upon the world necessitates the integration of body-related information from multiple sensory modalities. These multimodal body representations will be the focus of this work.

Over the years, several models have attempted to account for how the body is represented in the brain. Most of these acknowledge the need for multiple representations that may incorporate different sensorimotor combinations (e.g., visual, tactile, motor, proprioceptive) and serve distinct purposes (e.g., spatial localization, acuity, action). For example, some earlier accounts identify two body representations, the 'body image' and the 'body schema' (Gallagher, 1986; Tiemersma, 1982). Various authors have used these terms in different ways, and sometimes interchangeably (Fisher, 1968; Gibson, 1966; Head & Holmes, 1911; Kolb, 1959; Merleau-Ponty, 1962; Myers, 1967; Schilder, 1935; Schilder, 1923; Straus, 1970; Tiemersma, 1982). However, the currently accepted definitions posit a clear distinction between the two terms. The body image results from the body being perceived as an object of awareness. It is conscious and reflective, including not only sensory information pertaining to the body, but also prior knowledge about the body and attitudes toward it. The body schema, on the other hand, is a pre-reflective coordination of the body in space, including dynamic postural and proprioceptive states (Gallagher, 1986). The functional distinction between these two body models has been

supported by double dissociations in deafferented patients (Gallagher & Cole, 1995; Paillard, 1999). The body image and the body schema may be conceived of as body models subserving perception and action, respectively (Dijkerman & de Haan, 2007).

Yet others believe that a dyadic taxonomy of body models is insufficient. Sirigu and colleagues, for example, propose four different levels of body representation in the brain (Sirigu, Grafman, Bressler, & Sunderland, 1991). The first level consists of semantic and lexical knowledge about bodies, such as the names of body parts and the functional relations between them. The second level comprises a structural representation of bodies in general, including a visuo-spatial description of the locations and positions of body parts relative to each other and to the body as a whole. The third level is a dynamically updated representation of the actual position of one's own body, based on information from multiple sensory modalities, including visual, tactile, proprioceptive, and vestibular inputs. Finally, the fourth level consists of motor programs that contribute to the representation of the body in external space. Schwoebel and Coslett (2005) propose a similar 3-level model consisting of a lexical/semantic representation called the 'body image', a dynamically updated sensorimotor representation called the 'body schema', and a topological map of the human body based primarily on visual experience, which they call the 'body structural description.' Both these accounts break down the traditional dyadic model into further separable levels of body representation.

The dissociation between a visuo-spatial body representation and both motor and semantic/lexical representations is supported by cases of autotopagnosia, in which the patient is unable to point to body parts despite being able to use them and to identify their names and functions when the experimenter points to them (Buxbaum & Coslett, 2001; Denes, Cappelletti, Zilli, Dalla Porta, & Gallana, 2000; De Renzi & Scotti, 1970; Ogden, 1985; Sirigu et al., 1991). Furthermore, a dissociation between pure autotopagnosia, which is specific to localizing one's own body parts, and heterotopagnosia, a specific deficit in localizing the body parts of others,

lends support to a dissociation between a visuo-spatial description of the human body in general and a multimodal representation of one's *own* body, including somatosensory inputs (Auclair, Noulhiane, Raibaut, & Amarenco, 2009; Degos, Bachoud-Levi, Ergis, Petrissans, & Cesaro, 1997; Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003). Impairment at the structural, visuo-spatial level would be expected to disproportionately affect localization of others' body parts, as information from somatosensory modalities could compensate for the deficit when localizing one's own body parts. Because the multimodal level of representation consists of information specific to one's own body, impairment at this level should only affect localization of one's own body parts, particularly when the patient cannot rely on visual input for the task. Indeed, Felician and colleagues observed that their autotopagnosic patient was able to compensate for her deficit in pointing to her own body parts when she relied on visual rather than somatosensory cues (Felician et al., 2003).

II. Cortical regions involved in representing the body

Extrastriate visual cortex

In the lateral occipito-temporal visual cortex, two brain regions have been found to respond selectively to visual depictions of human bodies: the extrastriate body area (EBA) in the posterior inferior temporal sulcus (Downing, Jiang, Shuman, & Kanwisher, 2001) and the fusiform body area (FBA) on the posterior fusiform gyrus (Peelen & Downing, 2005). Both areas show a greater blood oxygen level-dependent (BOLD) response to images of whole human bodies and body parts than to other categories of images, such as non-human animals, inanimate objects, and scenes (Downing et al., 2001; Peelen & Downing, 2005; Taylor, Wiggett, & Downing, 2007). In addition, both the EBA and the FBA show an increased response to low-level depictions of human bodies, such as stick figures and silhouettes, relative to scrambled versions of these stimuli (Downing et al., 2001; Peelen & Downing, 2005). This indicates that

the selective response for human bodies is not due to the visual complexity of the body stimuli relative to the control stimuli. Furthermore, the EBA seems to be more selective for body parts, whereas the FBA responds preferentially to images of whole human bodies (Taylor et al., 2007). This suggests a division of labor between the two regions, wherein the EBA performs a parts-based analysis, while the FBA engages in more holistic, configural processing of human body forms.

The exact nature of the information processing performed by these regions is still debated. Studies showing an enhanced BOLD response in the right FBA to images of one's own body relative to the bodies of others (Hodzic, Muckli, Singer, & Stirn, 2009), and to the bodies of familiar relative to unfamiliar others (Hodzic, Kaas, Muckli, Stirn, & Singer, 2009), suggest that this region might discriminate body identity. One study found an enhanced response to one's own body compared to others' bodies in both the right EBA and the right FBA, though this difference was small compared to the difference between the response to intact and scrambled bodies, irrespective of identity (Vocks et al., 2010). Additional studies, however, also indicate that the right EBA might be sensitive to body identity. Using a functional magnetic resonance imaging (fMRI) adaptation approach, Myers and Sowden found separate sub-populations of neurons in the right EBA that were sensitive to images of either one's own or another person's body parts (Myers & Sowden, 2008). This might offer an alternative explanation for why classic BOLD analyses do not often detect a difference in EBA activation according to body identity, namely, that they did not provide a spatial resolution high enough to detect neuronal sub-populations preferentially responding to images of one's own body or the bodies of others. Other studies found differential BOLD responses in the right EBA to images of bodies presented from egocentric and allocentric viewpoints (Chan, Peelen, & Downing, 2004; Saxe, Jamal, & Powell, 2006). Together, these studies suggest that the right FBA, and possibly

the right EBA, might participate in a low level of body identity processing, distinguishing self from other and familiar from unfamiliar bodies.

Despite the EBA being located in visual cortex, some studies have implicated it in non-visual body processing. For example, the EBA is activated during haptic exploration of body parts (Costantini, Urgesi, Galati, Romani, & Aglioti, 2011; Kitada, Johnsrude, Kochiyama, & Lederman, 2009). Haptic body part recognition, despite being a somatosensory task, may engage a structural representation of the body that has primarily been developed through visual experience. In addition, the EBA is activated during the execution of limb movements, even in the absence of visual feedback, and to a greater extent than during motor imagery (Astafiev, Stanley, Shulman, & Corbetta, 2004; Ishizu, Noguchi, Ito, Ayabe, & Kojima, 2009; Orlov, Makin, & Zohary, 2010). However, the EBA's response during motor tasks could result from functional connections between the EBA and other brain regions involved in action execution rather than from action processing in the EBA itself. On the whole, both the EBA and the FBA appear to participate in a primarily visuo-spatial, structural representation of human bodies in general.

Primary motor and somatosensory cortices

In addition to the visual body areas in extrastriate cortex, motor and somatosensory representations of the body are located on the anterior and posterior banks of the central sulcus, respectively. Both areas exhibit somatotopic organization, with overrepresentation of areas that exhibit fine motor control or high sensitivity (Penfield & Rasmussen, 1950). The primary motor cortex (MI) on the pre-central gyrus contains pyramidal neurons with axons that descend to the spinal cord, where they synapse with spinal motor neurons that activate muscles to produce voluntary movement (Davidoff, 1990). The primary somatosensory cortex (SI) on the post-central gyrus encompasses Brodmann's areas 1 and 2 and Vogts' areas 3a and 3b (Zilles, 1990). It receives input from afferent nerve fibers via the thalamus. Areas 1 and 3b

receive information primarily from cutaneous afferents, while areas 2 and 3a receive input from proprioceptive afferents from the muscles and joints (Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Mountcastle, 1984). In addition to mapping the body for motor and somatosensory functions, there is some evidence that MI and SI may participate in representing the body at multiple levels. For instance, passive reading of action words performed by different effectors (e.g., the arm, the leg, or the tongue) is associated with somatotopic activation of MI and the adjacent premotor cortex (Hauk, Johnsrude, & Pulvermüller, 2004).

Posterior parietal cortex

Lying caudal to the post-central gyrus, the posterior parietal cortex processes body-related information from multiple sensory modalities. Single-unit recordings in monkeys have shown that area 5, the superior parietal lobule (SPL), encodes limb position from a combination of visual and proprioceptive inputs (Colby & Duhamel, 1991; Graziano, Cooke, & Taylor, 2000; MacKay & Crammond, 1987; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Sakata, Takaoka, Kawarasaki, & Shibusaki, 1973). Lesions of the human SPL impair the ability to perform reaching movements to targets (Karnath, 1997; Levine, Kaufman, & Mohr, 1978; Wolpert, Goodbody, & Husain, 1998). The SPL therefore appears to guide limb localization and movement in space, representing the body for the purpose of action.

A nearby area in the anterior and ventral portion of the intraparietal sulcus (IPS) also appears to process multisensory body-related information. Neurons in the monkey ventral intraparietal area (VIP) respond to visual, tactile, vestibular, and auditory information pertaining to the movement of the body or around the body (Avillac, Ben Hamed, & Duhamel, 2007; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Duhamel, Colby, & Goldberg, 1998; Schlack, Hoffmann, & Bremmer, 2002; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). Using fMRI, evidence for a similar multisensory body-centered representation

has been found in the human IPS (Bremmer et al., 2001; Gentile, Petkova, & Ehrsson, 2011; Makin, Holmes, & Zohary, 2007). The human VIP, similar to the SPL, might integrate information from multiple sensory modalities to encode the positions of body parts in space.

Insula

The previous sections have focused on aspects of bodily sensation and representation localizable in space, either in terms of the body surface, muscle groups, or external spatial coordinates. Other sensations arising from the body may be less spatially specific, instead providing information about the state of the body important for homeostatic regulation. These sensations fall under the category of 'interoception', which is generally considered to include hunger, thirst, air hunger, sexual arousal, and visceral sensations (Craig, 2002, 2009). Some also categorize cutaneous pain, itch, and thermal sensation as interoceptive, despite these sensations being localizable on the skin surface, as they are nonetheless part of the spinothalamocortical afferent pathway that conveys information about the physiological status of the body (Craig, 2002). The insula appears to be a key structure for interoception, as it plays a role in the processing of all these sensations (Banzett et al., 2000; Brooks, Zambreanu, Godinez, Craig, & Tracey, 2005; Brooks, Nurmikko, Bimson, Singh, & Roberts, 2002; Craig, Chen, Bandy, & Reiman, 2000; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Del Parigi et al., 2002; Egan et al., 2003; Farrell et al., 2006; Mochizuki et al., 2007; Morris & Dolan, 2001; Stoleru et al., 1999). Further studies suggest that the insula might be important for bodily awareness, integrating across interoceptive, exteroceptive, and affective domains (Craig, 2009; Simmons et al., 2013).

III. Multisensory interactions and body ownership

Normally, one's sense of body ownership occurs seamlessly. You know that your body is your own by virtue of occupying it and exerting control over it. Nevertheless, under certain

circumstances, the sense of body ownership can break down, revealing information about the underlying mechanisms that normally maintain it. In somatoparaphrenia, for example, patients with right fronto-parietal lesions deny ownership over a contralesional limb (see Vallar & Ronchi, 2009 for a review). This delusion of disownership persists despite these patients being able to see that the affected limb is attached to their body (Nielsen, 1938). Case studies of somatoparaphrenia are convergent with neuroimaging evidence that points to a right fronto-parietal network underpinning self-recognition (Uddin, Iacoboni, Lange, & Keenan, 2007).

In healthy participants without brain damage, manipulating body ownership is a more difficult task. One of the hallmarks of body ownership is that it is ever-present, i.e., it is “the same old body always there” (James, 1890). One popular approach has been to induce an illusion of owning an extra-corporeal object in the way that one would a body part, as in the rubber hand illusion (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Capelari, Uribe, & Brasil-Neto, 2009; Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Kammers et al., 2009; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Mohan et al., 2012; Moseley, Olthof, et al., 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris, Costantini, & Haggard, 2008; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Tsakiris & Haggard, 2005). In the classic rubber hand illusion, the participant’s hand is hidden behind a barrier with a false hand placed next to it. The experimenter then touches the participant’s real, hidden hand and the false hand in synchrony, resulting in an illusion that the false hand is the participant’s actual hand. In a control condition, the participant’s real hand and the rubber hand are touched in temporal asynchrony. This asynchronous condition is balanced with the synchronous condition in terms of the amount of visual and tactile stimulation, but it does not induce an illusion of owning the false hand.

Aside from a questionnaire assessing the subjective experience of the illusion, a common method for measuring the rubber hand illusion is to have the participant point to the location where they feel their real, hidden hand to be. After seeing the rubber hand touched in synchrony with their own, the perceived position of their real hand tends to shift toward the location of the rubber hand, an effect called proprioceptive drift (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). In this way, the rubber hand illusion is a prime example of how multisensory inputs interact to produce a coherent percept of one's own body. Vision of touch on the false hand captures the synchronous tactile sensations on the participant's own hand, and proprioception is recalibrated to bring information from the three senses into alignment (Tsakiris, 2010).

The rubber hand illusion has also demonstrated that embodiment is not a purely bottom-up process. If the rubber hand is replaced with an object that does not resemble a hand, synchronous visuo-tactile stimulation will rarely result in an embodiment illusion (Tsakiris et al., 2010, 2008; Tsakiris & Haggard, 2005; but see Armel & Ramachandran, 2003). This suggests that a structural body model is consulted to test the plausibility that the extra-corporeal object is in fact a body part (Tsakiris, 2010). Furthermore, the rubber hand illusion does not work if the false hand is placed in a posture incongruent with the posture of the participant's actual hand (Tsakiris & Haggard, 2005), indicating that the bottom-up correlation of visuo-tactile inputs also interacts with a dynamic, postural representation of the body to determine whether the object will be incorporated.

The rubber hand illusion paradigm has been extended to induce whole-body illusions using a virtual reality headset linked to a camera in a different location. In the first-person perspective version of the whole-body illusion, the participant looks down towards the front of their own body, which is being stroked by the experimenter, but sees the body of a mannequin that is being stroked in synchrony (Petkova & Ehrsson, 2008). In the third-person perspective

version, the camera is placed behind the participant so that they see their own body in front of them, inducing an out-of-body experience (Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). The whole-body illusion in the third-person perspective, like the rubber hand illusion, can be measured by proprioceptive drift. When participants simultaneously observe touch on the back of the body in front of them and feel the touch on their own back, they mislocalize themselves towards the location where they saw their body being stroked (Lenggenhager et al., 2007). These experiments indicate that similar multisensory processes underlie both the sense of whole-body ownership and embodiment of individual body parts.

Finally, a similar illusion has been found when participants view another person's face being touched in synchrony with touch on their own face (Bufalari, Lenggenhager, Porciello, Holmes, & Aglioti, 2014; Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013; Fini, Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013; Mazzurega, Pavani, Paladino, & Schubert, 2011; Paladino, Mazzurega, Pavani, & Schubert, 2010; Sforza, Bufalari, Haggard, & Aglioti, 2010; Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012; Tajadura-Jiménez, Lorusso, & Tsakiris, 2013; Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). In this "enfacement" illusion, synchronous visuo-tactile inputs update the mental self-face representation so that features of the other person's face are assimilated. The enfacement illusion will be discussed in greater detail in Chapter 4.

This family of illusions induced by synchronous visuo-tactile stimulation is a striking example of the multisensory processes behind the sense of body ownership for the body as a whole, for individual body parts, and for the face, which is a body part especially tied to our sense of self-identity (Devue & Brédart, 2011). Other lines of embodiment research have investigated more subtle interactions between sensory modalities carrying information about the body, in particular, between vision and cutaneous sensations. These interactions will be the primary focus of the present work. Chapter 1 will overview how merely viewing the body can

enhance spatial tactile acuity (Cardini, Haggard, & Làdavas, 2013; Cardini, Longo, Driver, & Haggard, 2012; Cardini, Longo, & Haggard, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard, Christakou, & Serino, 2007; Harris, Arabzadeh, Moore, & Clifford, 2007; Kennett, Taylor-Clarke, & Haggard, 2001; Konen & Haggard, 2014; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007; Serino, Padiglioni, Haggard, & Làdavas, 2009; Taylor-Clarke, Kennett, & Haggard, 2002, 2004). This was previously thought to occur outside the influence of higher-level representations of body identity, as spatial tactile acuity improves both when participants see their own body and when they see the body of another person. However, I will provide evidence that there are two pathways for visual enhancement of touch, a person (own-body) pathway and an interpersonal (other-body) pathway, that are at least partially distinct. Chapter 2 will then address how viewing the body affects pain perception. In a series of experiments, I applied a signal detection approach to determine whether vision of the body affects nociceptive sensitivity or post-perceptual pain judgments. I also investigated whether viewing the body alone and viewing a noxious event on the body modulate pain perception in distinct ways. Chapter 3 will return to interactions between vision and innocuous tactile sensation, and address the higher-order constraints on visual remapping of touch (Cardini, Costantini, et al., 2011; Cardini, Bertini, Serino, & Làdavas, 2012; Fini et al., 2013; Serino, Giovagnoli, & Làdavas, 2009; Serino, Pizzoferrato, & Làdavas, 2008), i.e., the conditions under which viewing another's face being touched does and does not improve detection of weak tactile stimuli on one's own face. Finally, in Chapter 4, I will examine how visuo-tactile interactions influence self-face recognition, a process that has traditionally been conceived of as a purely visual task (Devue & Brédart, 2011). To accomplish this, I will return to the enfacement illusion, and present evidence that this effect is not influenced by the emotional content of the other person's face. In particular, I will discuss this finding in light of the evidence for an asymmetric relationship between the processing of facial identity and facial

expressions (Ellamil, Susskind, & Anderson, 2008; Fox & Barton, 2007; Fox, Oruç, & Barton, 2008; Schweinberger & Soukup, 1998; Spangler, Schwarzer, Korell, & Maier-Karius, 2010).

Chapter 1: Visual enhancement of spatial tactile acuity

1.1. Visual enhancement of touch

A number of studies have now demonstrated that viewing the body can enhance tactile acuity on the seen body part, even if the tactile stimulation itself is invisible, or vision is non-informative about the tactile stimulus (Cardini, Haggard, et al., 2013; Cardini, Longo, et al., 2012, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard et al., 2007; Harris et al., 2007; Kennett et al., 2001; Konen & Haggard, 2014; Press et al., 2004; Serino et al., 2007; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002, 2004). This visual enhancement of touch (VET) is unlikely to be simply an effect of directing visuo-spatial attention because looking at a non-body object appearing in the same location as the body part does not improve tactile acuity relative to a control condition of complete darkness (Kennett et al., 2001; Serino, Padiglioni, et al., 2009). Rather, seeing the body part may activate a multisensory representation of the body that is able to modulate the activity of unimodal, somatotopically organized somatosensory cortex (Fiorio & Haggard, 2005; Konen & Haggard, 2014; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002).

Importantly, viewing the body relative to a non-body object seems to only enhance performance on *spatial* tactile acuity tasks. Studies demonstrating a VET effect have typically used either a two-point discrimination task (Kennett et al., 2001; Serino et al., 2007; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002) or a grating orientation discrimination task (Cardini, Haggard, et al., 2013; Cardini, Longo, et al., 2012, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Konen & Haggard, 2014; Taylor-Clarke et al., 2004), both of which require discriminating the spatial properties of the tactile stimuli. While viewing the body improves performance on these spatial discrimination tasks, it actually impairs performance on non-spatial tactile acuity tasks such as detection of near-threshold stimuli (Harris et al., 2007; Press et al., 2004). Although one study found accelerated detection of tactile stimuli when viewing the

hand (Tipper et al., 1998), the visual control condition in that experiment was the participant's other hand, separated from the stimulated hand in space, so the facilitation could have resulted from the orientation of spatial attention rather than from a specific effect of viewing the hand. On the whole, these studies indicate that the VET effect involves an enhancement of spatial tactile acuity in particular rather than a general facilitation of any tactile judgment. What is more, they suggest that the mechanism behind VET involves a sharpening of tactile receptive fields, which would be expected to improve performance on spatial discrimination tasks but not on simple detection tasks (Harris et al., 2007; Press et al., 2004).

Several lines of evidence suggest that viewing the body enhances spatial tactile acuity via modulation of primary somatosensory cortex (SI). First, viewing the arm compared to a non-body object during a spatial tactile acuity task increased the amplitude of the N80 event-related potential (ERP) component over scalp location C3, which has been attributed to late SI processing (Taylor-Clarke et al., 2002). Second, disrupting SI activity with single-pulse transcranial magnetic stimulation (TMS) in the interval between visual and tactile stimulation eliminated VET, whereas similar disruption of activity in the secondary somatosensory area (SII) had no effect on tactile acuity in either the view-hand or the view-object condition (Fiorio & Haggard, 2005). Finally, the VET effect seems to follow the somatotopic organization of SI. Viewing the hand enhances tactile acuity on both the hand and the face, which are represented in adjacent portions of the lateral aspect of SI, but it has no effect on tactile acuity on the foot, which is represented more medially (Serino, Padiglioni, et al., 2009).

Further studies have provided evidence in favor of the hypothesis that viewing the body enhances spatial tactile acuity by sharpening tactile receptive fields in early somatosensory cortex. When a two-point discrimination task is performed in the presence of vibro-tactile maskers at varying distances from the target tactile stimuli, viewing the body relative to a non-body object decreases the effect of distant maskers but increases the effect of nearby maskers (Haggard et al., 2007). Because a cutaneous masking stimulus will only impair perception of a

target stimulus if the two stimuli fall within the same tactile receptive field (Laskin & Spencer, 1979), this finding is consistent with a sharpening of receptive fields. In addition, viewing the hand increased the suppression of the somatosensory-evoked potential (SEP) produced by electrically stimulating the index and middle fingers simultaneously relative to stimulating each one individually (Cardini, Longo, et al., 2011). In other words, viewing the hand strengthened lateral inhibition within early somatosensory cortex. Lateral inhibition occurs because a cortical sensory neuron that fires will inhibit adjacent cortical sensory neurons via γ -aminobutyric acid (GABA)-ergic interneurons. This arrangement enhances spatial acuity because the smaller the stimulus (i.e., the higher its spatial resolution), the less lateral inhibition it will trigger from neighboring receptive fields (Cardini, Longo, et al., 2011). The finding that viewing the body increases somatosensory intracortical inhibition therefore offers a potential mechanism underlying visual modulation of early somatosensory receptive fields.

Though the aforementioned studies suggest that VET results from modulation of receptive field size in SI (Cardini, Longo, et al., 2011; Fiorio & Haggard, 2005; Haggard et al., 2007; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002), the source of this modulation is not well understood. According to one view, posterior parietal cortex may receive inputs from body-specific areas in the occipito-temporal visual cortex and then send feedback to SI that influences the corresponding part of the somatotopic map (Fiorio & Haggard, 2005; Kennett et al., 2001; Taylor-Clarke et al., 2002). This view is consistent with primate studies that identified multisensory body-centered representations from single-cell recordings in the monkey ventral intraparietal area (VIP). Neurons in this posterior parietal area responded to visual, tactile, vestibular, and auditory information pertaining to self-motion (Avillac et al., 2007; Bremmer et al., 2002; Duhamel et al., 1998; Schlack et al., 2002, 2005). Functional magnetic resonance imaging (fMRI) studies support the existence of a similar multisensory body-centered representation in the human intraparietal sulcus (IPS) (Bremmer et al., 2001; Gentile et al., 2011; Makin et al., 2007). Importantly, Makin and colleagues (2007) found a hand-centered

representation in the anterior IPS where visual, tactile, and proprioceptive inputs converge. Disrupting this area by delivering TMS during a brief interval between viewing one's own hand and receiving tactile stimulation eliminated VET (Konen & Haggard, 2014). The anatomical and temporal specificity of the disruptive effect suggests that the human ventral intraparietal area (hVIP) of the anterior IPS contributes to VET by providing a relay between visual and tactile cortices.

1.2. Own-body versus other-body: Same or different mechanisms?

The studies described above examined the effect of seeing *one's own* body on tactile acuity. Seeing the body of another person can also enhance spatial tactile acuity on the corresponding body part of the observer (Cardini, Haggard, et al., 2013; Haggard, 2006). Nevertheless, the mechanisms mediating VET in these two situations may be different, because they are differentially sensitive to spatial incongruence. VET was abolished when one's own hand was seen in a location incongruent with the hand's true location, suggesting that proprioceptive signals regarding spatial location contribute to personal (own-body) VET. However, when the viewed hand clearly belonged to another person, VET was obtained irrespective of whether the hand appeared at the proprioceptively sensed location of the participant's own hand or elsewhere (Cardini, Haggard, et al., 2013). Thus, personal VET relies on congruent proprioceptive information, and is therefore *inherently* self-referential (O'Shaughnessy, 1995). In contrast, the integration of congruent proprioceptive information is not required for interpersonal VET, when the seen hand belongs to another person.

This behavioral dissociation raises the possibility of two dissociable routes linking visual and somatosensory areas to produce VET. A self-specific route would pass through multisensory regions that also process proprioceptive signals, while the second, interpersonal route would pass through a set of intermediate relays insensitive to proprioceptive processing. Importantly, both routes might originate in a common visual source area; indeed, extrastriate occipital cortex contains visual areas that are specific for viewing bodies and body parts

irrespective of whether they belong to oneself or to another person (Chan et al., 2004; Downing et al., 2001; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Urgesi, Berlucchi, & Aglioti, 2004). Equally, both VET routes presumably converge on SI, which contains the key cortical circuitry underlying tactile acuity (Roland, 1987). Nevertheless, the neural mechanisms that mediate personal (own-body) and interpersonal (other-body) VET may be at least partially distinct, relying upon different sources of SI modulation.

Experiment 1: Dissociable routes for personal and interpersonal visual enhancement of touch

The hypothesis that there are dissociable routes for personal and interpersonal VET was tested by using transcranial magnetic stimulation to disrupt the intermediate relay for the personal route, the hVIP (Konen & Haggard, 2014). Changes to personal but not interpersonal VET from such disruption would support the dual route hypothesis. In another condition the EBA was disrupted in order to confirm that both routes have a common visual source in body-specific areas of the occipital cortex. Participants performed a tactile acuity task while viewing high-quality visual images of their own hand, another person's hand, and a non-body object. Prior to the tactile acuity task, participants underwent continuous theta-burst stimulation (cTBS) to suppress the left hVIP, a multisensory area implicated as a source of SI modulation in personal VET (Konen & Haggard, 2014) but untested as of yet in interpersonal VET. It was hypothesized that temporarily disrupting the hVIP would eliminate enhancement of tactile acuity at the sight of one's own hand but leave enhancement at the sight of another's hand intact. In a further session, cTBS was applied over the EBA, a region in the lateral occipito-temporal cortex involved in the visual processing of human bodies (Downing et al., 2001; Pitcher et al., 2009; Urgesi et al., 2004). The EBA appears either insensitive (Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009) or only minimally sensitive (Vocks et al., 2010) to whether

one's own body or another's body is viewed. It was thus predicted that disrupting the EBA would affect both personal and interpersonal VET, indicating that it provides a common visual source for VET, before the personal and interpersonal routes divide.

Method

Participants

Twenty-six volunteers (19 female, 21-30 years old) participated in the experiment after being screened for contraindications to TMS (Rossi, Hallett, Rossini, Pascual-Leone, & The Safety of TMS Consensus Group, 2009; Wassermann, 1998). They gave written informed consent to participate in the experiment and were tested in accordance with the ethical standards of the 1964 Declaration of Helsinki. The study was approved by the Ethics Committee for Psychological Research and the Bioethics Committee of the University of Bologna.

Materials

To produce images of participants' hands and the other-hand stimuli (which were the hands of 5 female and 5 male volunteers who did not participate in the experiment), a photograph of the right hand with the palm facing down was taken with a digital camera and placed on a black background in Adobe Photoshop CS3. A laptop computer running Presentation 0.60 was used to display the visual stimuli on a standard 4:3 ratio, 15-inch screen, to send auditory cues via earphones to the experimenter who delivered tactile stimulation, and to collect participants' responses.

TMS was delivered with a Magstim Rapid² figure-of-eight coil. A Biopac MP35 system was used to acquire electromyographic activity while each participant's resting motor threshold was determined. Neuronavigation was conducted with an NDI Polaris Vicra system and SofTactic Evolution 1.2 software.

The grating orientation task employed a set of plastic, circle-sectional square-wave gratings with alternating ridges and grooves of equal widths (Van Boven & Johnson, 1994).

Ridge and groove widths varied between gratings from 0.50 mm to 2.00 mm in intervals of 0.25 mm. The smaller the width of the ridges and grooves, the more difficult it is to discriminate their orientation.

Procedure

Prior to the experiment, participants came to the laboratory for a preparatory session. During this session, each participant's grating orientation discrimination threshold was determined. Beginning with the largest ridge width (2.00 mm), the experimenter repeatedly applied the grating to the tip of the right middle finger in randomly selected orientations (horizontal/across the finger or vertical/along the finger) for approximately 0.5 s per application. The participant's hand was hidden from view under a box with an opening at the back so the experimenter could apply the gratings. A computer screen placed face-up on top of the box showed a rectangle on a black background that the participant fixated while indicating whether the grating orientation was horizontal or vertical. This procedure continued with gratings of decreasing ridge width until the participant answered correctly on 55-65% of 40 trials for a given ridge width. This grating ($M_{\text{width}} = 0.74$ mm, $SD_{\text{width}} = \pm 0.18$ mm across participants) was then used in the subsequent experimental sessions. Next, each participant's resting motor threshold (RMT) was determined using single pulses of TMS, with the coil handle pointed backwards and at 45 degrees relative to the midline, to locate the hand area of the left primary motor cortex and determine the stimulator output level required to elicit motor-evoked potentials of at least 50 μ V from the right first dorsal interosseous hand muscle in 5 out of 10 trials ($M_{\text{RMT}} = 54.23\%$, $SD_{\text{RMT}} = \pm 8.86\%$). Then, neuronavigation software was used to create an estimated magnetic resonance imaging volume for each participant for use in locating the left hVIP and EBA. Finally, participants had a photograph taken of their right hand with the palm facing down, and then rated the similarity of their own hand to the other-hand stimuli (gender-matched) on a scale from 1 ("looks nothing like my own hand") to 6 ("looks very much like my own hand"). The lowest-rated hand was used as the other-hand stimulus in the experimental sessions to ensure

that participants were able to distinguish the image of their own hand from the image of the other person's hand. The similarity rating of the other-hand stimulus was never higher than 2.

Participants underwent three experimental sessions on separate days. In one session, participants received cTBS over the left hVIP at Talaraich coordinates $x = -35$, $y = -51$, $z = 42$ (Konen & Kastner, 2008) with the coil handle pointing backwards and at 45 degrees to the midline. In another session, cTBS was delivered over the left EBA with the handle pointing directly backwards and towards the midline. The left EBA was localized by using the average Talaraich coordinates ($x = -47$, $y = -72$, and $z = 7$) from 22 studies using functional localizers (as reported by de Gelder et al., 2010). In the sham session, the coil was placed over the left hVIP but rotated 90 degrees in a vertical plane. The sessions were otherwise identical, and session order was counterbalanced. At the beginning of each experimental session, neuronavigation data were used to locate the target site. Then the experimenter administered 20 grating discrimination trials using the ridge width selected in the preparatory session. If the participant answered correctly on more than 65% or less than 55% of trials, the procedure used in the preparatory session to determine the orientation discrimination threshold was repeated. Next, cTBS (3 pulses at 5 Hz, repeated at 50 Hz intervals) was delivered over the target site for 40 s (600 pulses total), a procedure that has been shown to suppress neural activity in the underlying cortical area for 60 min (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Stimulator output level was set to 70% of the RMT found in the preparatory session.

After a 5-minute pause, participants then underwent two blocks (60 trials each) of the grating orientation task (5 s per trial, 5 min per block). The blocks were separated by a few minutes of rest during which the orientation discrimination threshold was re-checked. As in the preparatory session, the participant's right hand was hidden under a box with a screen on top where visual fixation was maintained. Each trial began with a fixation cross on a black background and an auditory cue to the experimenter's headphones indicating which orientation to deliver at visual stimulus onset. After 2 s, an image of the participant's own hand, another

person's hand, or a wooden block appeared on the screen for 3 s, along with another auditory cue to the experimenter signaling the time to touch the grating to the participant's middle fingertip. The second auditory cue allowed the experimenter to be blind to the visual stimulus condition, because tactile stimulation could be synchronized with the onset of the visual stimulus without looking at the screen. Each visual stimulus (own-hand, other-hand, and wooden block) was presented 20 times in each block in a random sequence. The two grating orientations were also presented randomly and equiprobably with each visual stimulus. Participants used a mouse with their left hand to indicate whether the grating orientation was horizontal (left button) or vertical (right button) on each trial. A schematic drawing of the experimental setup is shown in Figure 1.1.

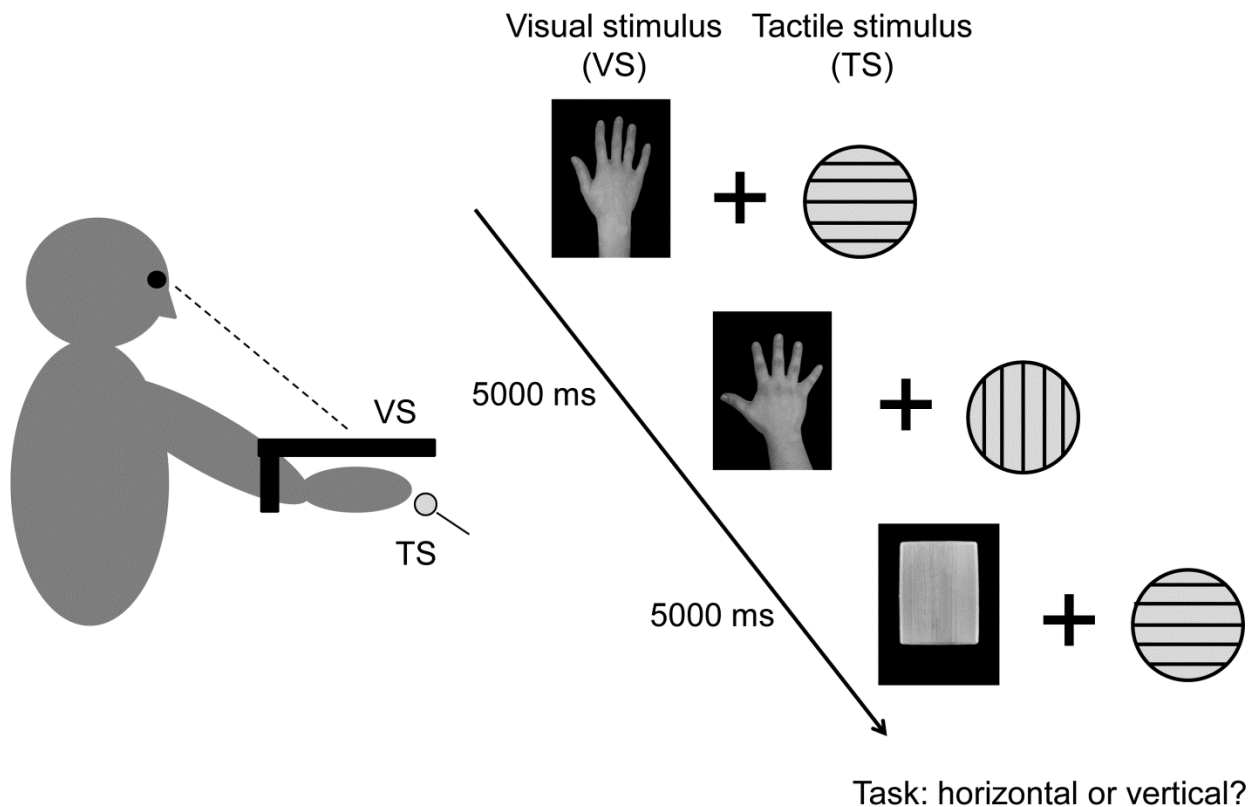


Figure 1.1. Diagram of the visual enhancement of touch (VET) paradigm showing delivery of the visual stimulus (VS) and the tactile stimulus (TS).

Design and Analysis

This experiment used a 3 x 3 factorial repeated measures design with the independent variables visual stimulus type (own-hand, other-hand, or wooden block) and TMS condition (hVIP, EBA, or sham stimulation). The dependent measure was the proportion of correct grating orientation judgments in each condition.

Results

To examine the effects of TMS on VET, a 3 (TMS target: hVIP, EBA, or sham) x 3 (visual condition: own-hand, other-hand, or object) repeated measures analysis of variance (ANOVA) was conducted on tactile grating orientation discrimination accuracy. Mauchly's tests were not significant (TMS target: $p = .140$; visual condition: $p = .677$; TMS target x visual condition interaction: $p = .555$), so no sphericity corrections were applied. There was neither a main effect of TMS target, $F(2, 50) = 1.51$, $p = .232$, partial $\eta^2 = .057$, nor a main effect of visual condition, $F(2, 50) = 2.38$, $p = .103$, partial $\eta^2 = .087$. Crucially, there was a highly significant interaction between visual condition and TMS target, $F(4, 100) = 3.63$, $p = .008$, partial $\eta^2 = .127$ (Figure 1.2).

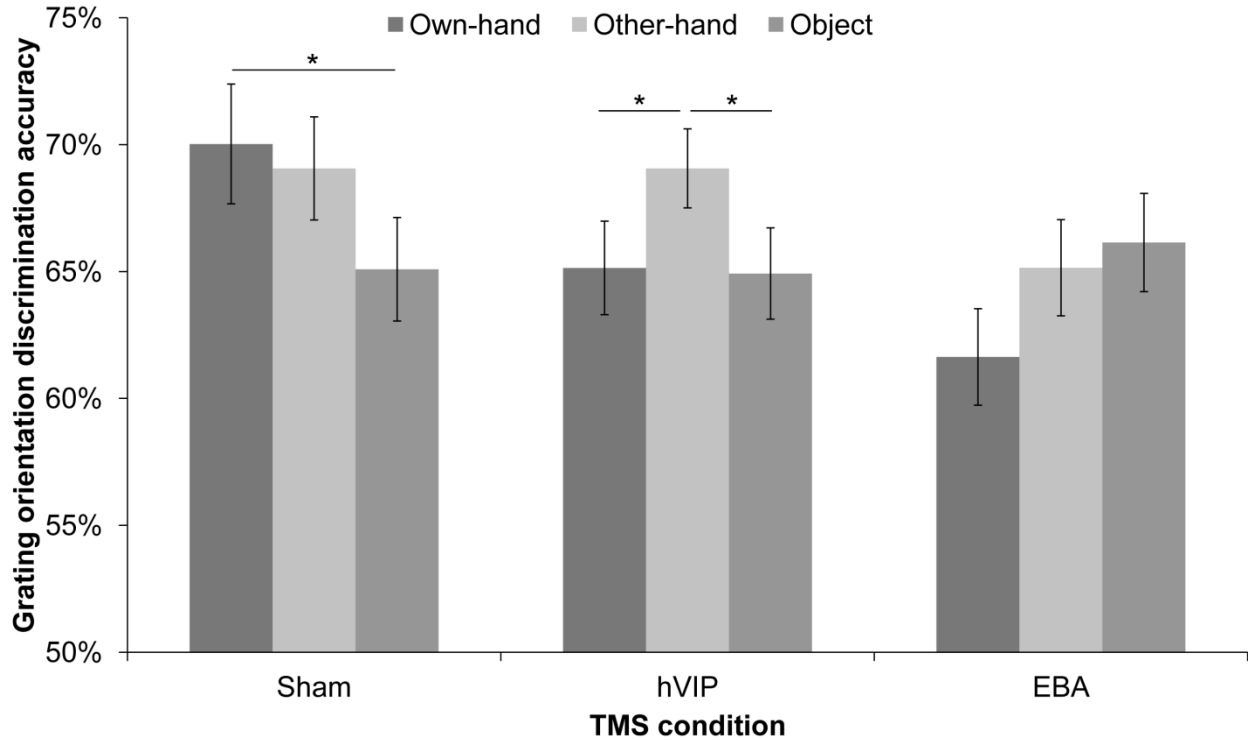


Figure 1.2. Mean (\pm SEM) accuracy of tactile grating orientation discrimination in each visual condition (own-hand, other-hand, and object) and TMS condition (sham, hVIP, and EBA). * = $p < .050$.

To elucidate the nature of this interaction, separate ANOVAs with the factor ‘visual condition’ (own-hand, other-hand, or object) were conducted for each TMS session. Significant ANOVAs were then followed up with paired-samples t-tests. In the sham condition, the effect of visual condition was significant, $F(2, 50) = 3.36, p = .043, \text{partial } \eta^2 = .119$. Pairwise comparisons of means were used to explore the sources of this effect. Such comparisons between three conditions do not require correction for multiple comparisons when the overall ANOVA is significant (Cardinal & Aitken, 2006). Participants were better at discriminating grating orientations when viewing their own hand ($M = 70.03\%, SEM = \pm 2.36\%$) than when viewing the object ($M = 65.09\%, SEM = \pm 2.04\%$), $t(25) = 2.58, p = .016$. Thus, the basic VET effect was replicated in the sham condition. Tactile acuity was also marginally better when

viewing the other person's hand ($M = 69.07\%$, $SEM = \pm 2.03\%$) than when viewing the neutral object, $t(25) = 1.98$, $p = .059$. There was no significant difference in accuracy between the own-hand and other-hand conditions, $t(25) = .45$, $p = .654$. This pattern of results replicates previous studies that have found enhancement of spatial tactile acuity both when viewing one's own hand and when viewing another person's hand (Cardini, Haggard, et al., 2013; Haggard, 2006).

Following TMS over the hVIP, the effect of visual condition was also significant, $F(2, 50) = 3.60$, $p = .035$, partial $\eta^2 = .126$. Accuracy was higher in the other-hand condition ($M = 69.07\%$, $SEM = \pm 1.56\%$) than in both the object condition ($M = 64.92\%$, $SEM = \pm 1.80\%$), $t(25) = 2.08$, $p = .048$, and the own-hand condition ($M = 65.15\%$, $SEM = \pm 1.84\%$), $t(25) = -2.15$, $p = .041$. There was no difference in accuracy between the own-hand and object conditions, $t(25) = 0.17$, $p = .869$. This corroborates the hypothesis that disrupting the hVIP would eliminate personal VET but leave interpersonal VET intact.

After TMS over the EBA, there was no effect of visual condition, $F(2, 50) = 2.63$, $p = .082$, partial $\eta^2 = .095$ (Own-hand: $M = 61.63\%$, $SEM = \pm 1.90\%$; Other-hand: $M = 65.15\%$, $SEM = \pm 1.89\%$; Object: $M = 66.14\%$, $SEM = \pm 1.94\%$). Thus, no follow-up comparisons were made. This supports the hypothesis that inhibiting the EBA would prevent both personal and interpersonal VET.

Discussion

The sham stimulation condition replicated previous findings that viewing either one's own hand or another person's hand could enhance tactile acuity (Cardini, Haggard, et al., 2013; Cardini, Longo, et al., 2012, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard et al., 2007; Harris et al., 2007; Kennett et al., 2001; Konen & Haggard, 2014; Press et al., 2004; Serino et al., 2007; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002, 2004). Disrupting the hVIP within the anterior IPS reduced the enhancement of tactile acuity found when participants viewed their own hand, but not when they viewed another person's hand. This suggests that the neural pathways underlying personal and interpersonal VET are at least

partially separate. Viewing one's own hand and another's hand might activate distinct body representations in the brain that enhance tactile perception by independent converging influences on somatosensory areas. One important difference between the effects of viewing one's own body or another person's body could lie in the contribution of proprioceptive information. A previous study showed that personal VET, but not interpersonal VET, involved integration of congruent visual and proprioceptive inputs (Cardini, Haggard, et al., 2013). The results of Experiment 1 suggest that this integration of proprioceptive and visual information occurs in a cortical pathway that includes the hVIP. This is consistent with a previous fMRI study that found evidence for converging visual, tactile, and proprioceptive signals in a hand-centered representation of space in the anterior IPS (Gentile et al., 2011; Makin et al., 2007).

A previous study (Konen & Haggard, 2014) showed that single-pulse TMS over the hVIP reduced personal VET. The results in the own-hand condition replicate and extend that finding in some important ways. The present study used an offline theta-burst TMS protocol, while the previous one used event-locked single-pulse TMS. Whereas the single-pulse TMS study confirmed that neural activity in the hVIP is causally relevant to personal VET, the present study confirms that the hVIP is a potential site of *enduring modulation* in the multisensory circuit underlying VET. Crucially, as discussed above, Experiment 1 also showed that the hVIP is involved in personal but not interpersonal VET, suggesting that the mechanism behind this multisensory interaction depends on the identity of the viewed hand.

Theta-burst suppression is thought to recruit long-term potentiation and long-term depression-like mechanisms in the stimulated cortical area, thus inducing plastic changes in cortical circuits (Huang et al., 2005). A recent study identified important individual differences in susceptibility to the effects of motor cortical cTBS (Hamada, Murase, Hasan, Balaratnam, & Rothwell, 2013), with no overall group effects. Nevertheless, this is not a concern for the interpretation of the present study, which found group-level effects of both hVIP and EBA stimulation.

Suppressing the EBA eliminated both personal and interpersonal VET, consistent with the idea that this area processes visual input from both one's own body and the bodies of others (Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009; Vocks et al., 2010). Importantly, this also shows that appropriately targeted cTBS is able to modulate interpersonal VET. While the EBA is considered a visual area, the possibility that it contributes to non-visual functions has been suggested before (Astafiev et al., 2004; Costantini et al., 2011; Ishizu et al., 2009; Kitada et al., 2009; Orlov et al., 2010). The results of the Experiment 1 suggest that visual representations of the body in the EBA make an important contribution to multisensory processing, in this case visual modulation of touch. The EBA result also helps to exclude some alternative interpretations of the effect of TMS over hVIP on VET. In particular, it suggests that the selective inhibition of personal but not interpersonal VET by theta-burst stimulation of the hVIP is unlikely to reflect an inability to modulate interpersonal VET because of any general factor associated with cTBS, such as participant expectation, or because of a general resilience of processing associated with the self.

Of the four independent levels of body representation proposed by Sirigu and colleagues (1991), two are particularly relevant in interpreting the results of Experiment 1: the visuo-spatial level (a structural representation of bodies in general) and the dynamic level (an online, multisensory representation of one's own body that updates with body posture and movement). Sirigu and colleagues argued for the independence of these two body representations based on a double dissociation between pure autotopagnosia—an inability to point to one's own body parts without an accompanying deficit in pointing to the body parts of others—and an inverse pattern of impaired and intact abilities in heterotopagnosia (Degos et al., 1997; Felician et al., 2003; Felician & Romaguère, 2008). The results of Experiment 1 can be accommodated within the same framework. Viewing hands may activate a visuo-spatial body representation regardless of the body to which the hands are attributed. Disrupting the EBA inhibited both personal and interpersonal VET, suggesting that this common visuo-spatial representation is

housed in the EBA, or in another structure receiving input from the EBA. However, only the sight of one's own hand, not that of another person, should activate a body representation dynamically updated with posture and movement (Cardini, Haggard, et al., 2013). The results of Experiment 1 suggest that the hVIP may house this representation. Importantly, this dissociation is made in the context of a somatosensory perceptual task. These different body representations may therefore represent distinct but converging influences that participate in top-down modulation of perception (cf. Konen & Haggard, 2014). The hVIP appears to be an area where somatosensory and visual inputs converge to bind visuo-spatial representations of bodies with dynamic proprioceptive and tactile descriptions of one's own body.

Experiment 1 yielded a single dissociation between the personal and interpersonal VET routes by demonstrating that the hVIP participates in the enhancement of tactile acuity when viewing one's own hand but not when viewing another's hand. However, the modulatory source responsible for interpersonal VET remains to be determined. One possibility could be another posterior parietal area that represents human bodies in terms of visuo-spatial configuration but without reference to exclusively self-originating sensory inputs such as proprioception. Lesion studies (Degos et al., 1997; Felician et al., 2003) and fMRI studies (Felician et al., 2009) suggest that the left angular gyrus (AG) of the inferior parietal lobule is involved in a visuo-spatial representation of the human body in general. In particular, damage to this area produces heterotopagnosia, a deficit in pointing to the body parts of others without accompanying impairments in naming them or in pointing to or naming one's own body parts (Degos et al., 1997; Felician et al., 2003). This indicates preserved semantic knowledge of human body parts, but an inability to place them within an extrapersonal visuo-spatial context.

A visuo-spatial body representation in the left AG might contribute to VET when viewing another person's hand. Activation of the left inferior parietal lobule has been observed in response to viewing body part actions (Buccino et al., 2001; Grèzes, Costes, & Decety, 1999), and there is also some evidence for processing of static visual body part stimuli in this region

(McCarthy, Puce, Belger, & Allison, 1999). The left inferior parietal lobule has extensive anatomical and functional connections with the occipital and temporal lobes, through which it could receive visual information. It is also connected to other regions of parietal cortex, including the postcentral gyrus, where SI is located (Wang et al., 2012). Other studies, in contrast, suggest that the AG may be involved in representing one's own body. Both neuroimaging (Spitoni, Galati, Antonucci, Haggard, & Pizzamiglio, 2010) and brain stimulation studies (Spitoni et al., 2013) have suggested a role for the AG in tactile distance judgments that refer to a mental representation of one's own body. However, both studies linked this own-body-referencing to the *right* AG, leaving the possibility that the left AG might be involved in visuo-spatial but not somatosensory body processing. Future research is needed to examine whether the left AG might be the source of SI modulation in interpersonal VET.

The point at which the pathways for personal and interpersonal VET diverge also remains to be determined. Experiment 1 demonstrated that the EBA is common to both personal and interpersonal routes. Whether the bifurcation point occurs within the EBA or further along the information processing pathway is unknown. There is some evidence that sub-populations of neurons in the right EBA are sensitive to either one's own body parts or the body parts of others, consistent with a role for the EBA in sorting visual body stimuli according to identity (Myers & Sowden, 2008). Note that this would not contradict the finding that the EBA is common to both personal and interpersonal VET, as the offline cTBS procedure that was used would be expected to suppress activity in neuronal sub-populations processing both own-body and other-body stimuli.

The right EBA also responds differentially to body parts presented in egocentric and allocentric viewpoints (Chan et al., 2004; Saxe et al., 2006), which could be an indicator of ownership. Chan and colleagues (2004) did not find a differential BOLD response to self-body versus other-body images. However, this could be due to the lower sensitivity of the standard region-of-interest fMRI contrast they used compared to Myers and Sowden's (2008) adaptation

approach, which allowed the latter to distinguish the response properties of distinct neuronal sub-populations within the EBA. One study, however, found differential responses to one's own body and the bodies of others in the right EBA (Vocks et al., 2010). Thus, the EBA might visually discriminate the bodies of oneself and others, marking the bifurcation point of the two routes. However, this speculation must be tempered by the consideration that the above studies found evidence for own-body and other-body selectivity in the right EBA, not the left EBA. The present results suggest that the left EBA houses a *common* visual representation of the human body without regard to ownership or identity. In that case, the personal and interpersonal routes would bifurcate later in the processing stream. For example, one model (Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009) proposes that body identity is discriminated in the fusiform body area, a body-responsive region located ventrally to the EBA.

Though viewing both one's own body and another's body enhances spatial tactile acuity, this enhancement is accomplished via distinct neural mechanisms (Figure 1.3). This suggests that common behavioral effects of viewing one's own and others' bodies need not indicate a shared *neural* representation. Reviewing the evidence for shared body representations, de Vignemont (2014) proposed that the appearance of common own-body and other-body activations may result from the two representations time-sharing some basic body information processing components (e.g., body part configuration) without entailing a complete self-other overlap. The results of Experiment 1 suggest that the visual body information processed in the EBA may be one shared component (but see Myers & Sowden, 2008 for contrary evidence), whereas the hVIP is specific to a representation of one's own body, perhaps because of its integration of proprioceptive input.

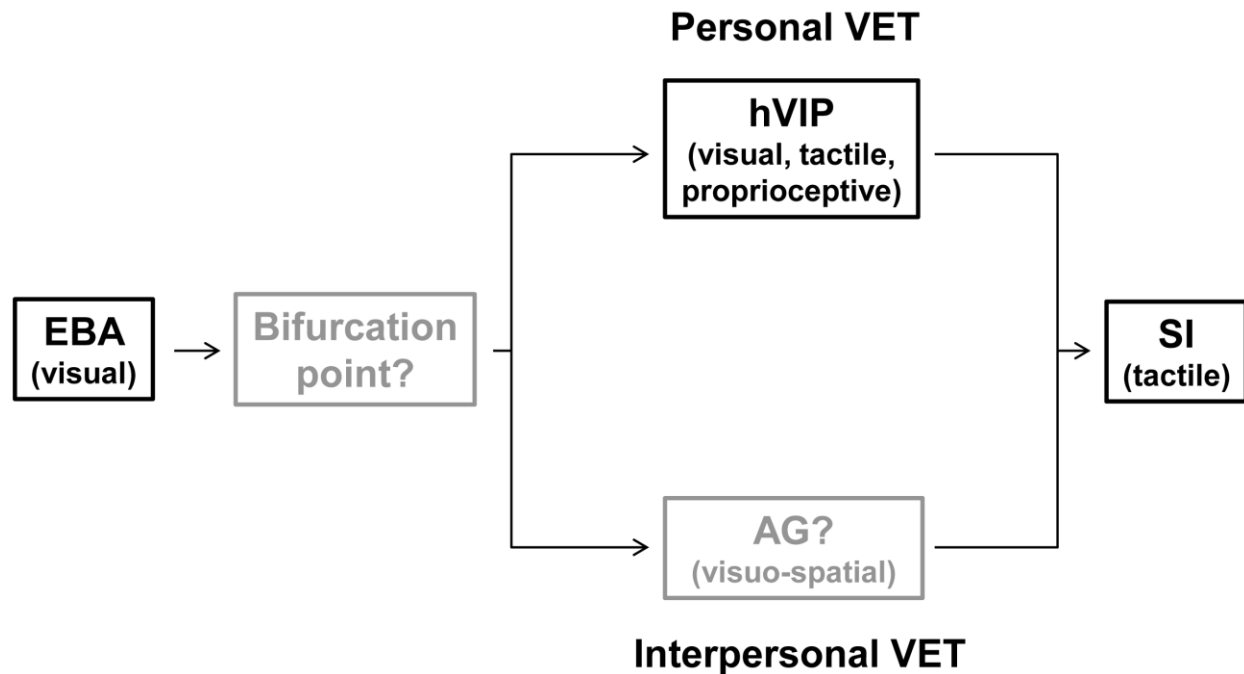


Figure 1.3. Model of the personal and interpersonal VET routes, based on evidence from previous studies (Fiorio & Haggard, 2005; Konen & Haggard, 2014) and the present study. Areas shown in gray have yet to be confirmed.

Conclusion

The present study suggests that personal VET, but not interpersonal VET, depends upon modulation from the multisensory hVIP. VET, a seemingly low-level crossmodal interaction, is in fact sensitive to the identity of the viewed body part. This sensitivity may reflect the strong tactile and proprioceptive inputs to the key VIP node of the personal VET circuit. This form of multisensory interaction does not, therefore, involve a ‘mirror system’ that maps both one’s own body and the bodies of others onto the same neural circuitry (cf. Decety & Sommerville, 2003; Gallese, 2001). Personal and interpersonal VET effects appear to rely upon distinct crossmodal mechanisms rather than completely overlapping representations of the body in the brain.

While it is clear that viewing the body enhances discrimination of the spatial properties of tactile stimuli, less is known about how viewing the body affects discrimination of the sensory properties of noxious stimuli, which are processed in a sensory system largely distinct from the system that processes innocuous tactile input. This issue will be the subject of the three experiments presented in Chapter 2.

Chapter 2: Visual modulation of pain perception

2.1. Pain and body representation

Pain is the conscious experience of nociception, a sensory system dedicated to the perception of stimuli that threaten the integrity of the bodily tissues (IASP Task Force on Taxonomy, 1994). It is unique among the bodily senses in that it possesses a strong motivational component in addition to being a sensory process. In fact, pain is often considered to have interacting sensory/discriminative, affective/motivational, and cognitive/evaluative dimensions (Melzack & Casey, 1968). The sensory/discriminative dimension comprises low-level perceptual features of nociceptive stimuli, such as location, intensity, timing, and sensory quality. The affective/motivational dimension highlights the aversive quality of pain that motivates pain avoidance behaviors. Finally, the cognitive/evaluative dimension refers to higher-order appraisal, learning, and control of pain.

As discussed in the introduction, pain is sometimes classified as an interoceptive sense because it conveys information about the physiological status of the body (Craig, 2002). Nonetheless, cutaneous pain also has properties of an exteroceptive sense, as it can be localized within a somatotopic reference frame. For this reason, some have proposed that the sense of pain lies on the boundary between interoception and exteroception (Haggard, Iannetti, & Longo, 2013). Its content is the body itself, but it has a spatial organization suitable for localizing external sources of noxious sensations. In this way, pain provides information about both the physiological state of the body, as well as external objects that may threaten the body's integrity.

Cutaneous pain is relayed by nociceptive afferents—small-diameter, thinly myelinated A δ and unmyelinated C fibers (Bessou & Perl, 1969; Burgess & Perl, 1967; Perl, 1968)—that project to the dorsal horn of the spinal cord (Christensen & Perl, 1970; Kumazawa & Perl, 1978;

Light & Perl, 1979; Sugiura, Lee, & Perl, 1986) and then to the brain via the spinothalamic pathway (Willis, Kenshalo, Jr., & Leonard, 1979). From the thalamus, these afferents project to various parts of the cortex, but predominately to the posterior insula, the medial parietal operculum, and the mid-cingulate cortex (Dum, Levinthal, & Strick, 2009). In accordance with structural connectivity, imaging studies have shown that cortical pain processing is not limited to a single structure. Instead, a distributed network of brain regions—often called the ‘pain matrix’—participates in pain perception, including SI, SII/parietal operculum, the insula, the anterior cingulate cortex (ACC), and the prefrontal cortex (see Apkarian, Bushnell, Treede, & Zubieta, 2005 for a review). Moreover, single neurons that respond to noxious stimuli but not to innocuous stimuli have been found in SI (Kenshalo, Jr., Chudler, Anton, & Dubner, 1988; Kenshalo, Jr. & Isensee, 1983), the parietal operculum (Dong et al., 1989), and the ACC (Hutchison, Davis, Lozano, Tasker, & Dostrovsky, 1999; Koyama, Tanaka, & Mikami, 1998; Sikes & Vogt, 1992; Yamamura et al., 1996).

2.2. Cortical regions involved in pain

Primary somatosensory cortex (SI)

Non-human primate studies have revealed nociceptive projections from the thalamus to SI, providing a pathway for nociceptive inputs to reach the sensory cortex (Gingold, Greenspan, & Apkarian, 1991; Kenshalo, Jr., Giesler, Leonard, & Willis, 1980; Rausell & Jones, 1991). SI nociceptive neurons have receptive fields appropriate for discriminating the location, intensity, and temporal characteristics of noxious stimuli (Kenshalo, Jr. et al., 1988; Kenshalo, Jr. & Isensee, 1983), suggesting a role for SI in processing the sensory dimension of pain. Nonetheless, relatively few nociceptive neurons have been found in SI compared to the number of neurons there that respond to innocuous somatosensory stimulation.

In humans, some forms of chronic pain are associated with disinhibition of the primary motor and somatosensory cortices (Eisenberg et al., 2005; Lefaucheur, Drouot, Ménard-Lefaucheur, Keravel, & Nguyen, 2006; Lenz et al., 2011; Schwenkreis et al., 2003) and with disorganization of SI somatotopic maps (Flor et al., 1995; Flor, Braun, Elbert, & Birbaumer, 1997; Maihöfner, Handwerker, Neundörfer, & Birklein, 2003; Tecchio, Padua, Aprile, & Rossini, 2002; Wrigley et al., 2009). Human brain imaging studies, however, have yielded inconsistent results regarding the role of SI in cortical pain processing, though this may be due to extraneous factors such as anatomical variability across participants or differences in statistical methods (for reviews, see Apkarian et al., 2005; Bushnell et al., 1999). Recently, a phase-encoded fMRI study found fine-grained somatotopic mapping of nociceptive stimulation in the SI hand area, comparable to that for innocuous tactile stimulation (Mancini, Haggard, Iannetti, Longo, & Sereno, 2012). Additionally, gamma-band oscillations arising from SI correlate with reported pain intensity independently of stimulus novelty or salience (Gross, Schnitzler, Timmermann, & Ploner, 2007; Zhang, Hu, Hung, Mouraux, & Iannetti, 2012), suggesting a close association between SI and pain perception.

Operculo-insular cortex

The parietal operculum (including SII) and the nearby posterior insular cortex are consistently activated in human imaging studies of pain perception (Apkarian et al., 2005; Garcia-Larrea, 2012). Together, the posterior insula and medial operculum (PIMO) receive 70% of spinothalamic cortical projections in monkeys, whereas SI receives less than 5% (Dum et al., 2009). The insula exhibits somatotopic organization of nociceptive input (Brooks et al., 2005; Henderson, Gandevia, & Macefield, 2007; Mazzola, Isnard, Peyron, Guénot, & Mauguière, 2009), though this insular somatotopy is not as finely grained as that found in SI (Mancini, Haggard, et al., 2012). Importantly, the PIMO is the only part of the cortex where direct stimulation induces acute pain, albeit only about 10% of the time (Mazzola, Isnard, Peyron, &

Mauguière, 2012). Moreover, the PIMO is the only cortical area where lesions result in selective loss of acute pain and temperature sensation, sometimes accompanied by chronic neuropathic pain (Garcia-Larrea, 2012). These observations provide strong evidence for the involvement of the PIMO in pain perception, leading some to identify the PIMO as the primary sensory cortex for nociception (Garcia-Larrea, 2012; Garcia-Larrea & Peyron, 2013).

Anterior cingulate cortex (ACC)

Neurons responding to nociceptive stimuli have been identified in area 24 of the ACC in both animals (Koyama et al., 1998; Sikes & Vogt, 1992; Yamamura et al., 1996) and pre-surgical human volunteers (Hutchison et al., 1999). The receptive fields of these neurons are large, often responding to nociceptive stimuli presented anywhere on the body surface (Sikes & Vogt, 1992; Yamamura et al., 1996), though limited spatial organization was identified in a small number of human participants (Hutchison et al., 1999). Interestingly, some nociceptive ACC neurons also respond in anticipation of a painful stimulus (Hutchison et al., 1999; Koyama et al., 1998). This suggests that the ACC is not a primary sensory area for pain, but may participate in the motivational component of pain perception.

Further evidence for the involvement of the ACC in the affective/motivational dimension of pain comes from rodent behavioral studies. Lesions of the rostral ACC in rats diminished a learned behavior known to reflect the affective component of pain (formalin-induced conditioned place avoidance) but did not affect acute nociceptive-related behaviors, such as paw lifting, licking, and flinching (Gao, Ren, Zhang, & Zhao, 2004; Johansen, Fields, & Manning, 2001). Observations of human chronic pain patients treated with cingulotomy also support this idea. These patients reported that they could still feel the pain, but it no longer bothered them (Foltz & White, 1962). In other words, lesioning the cingulate cortex eliminated the aversive quality of pain without disrupting the pain sensation itself. In healthy human participants, hypnotic

suggestions that selectively reduced the unpleasantness of acute noxious stimuli without altering their perceived intensity revealed changes in pain-evoked activity in the ACC (Rainville, Duncan, Price, Carrier, & Bushnell, 1997). These studies indicate that the dimension of pain encoded by the ACC is affective rather than sensory in nature.

Both single-unit recordings (Hutchison et al., 1999) and fMRI (Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Singer et al., 2004) have demonstrated that areas of the ACC activated by noxious stimuli also respond to the observation of another person receiving noxious stimulation. Moreover, neurons in the ACC anticipate noxious stimuli (Hutchison et al., 1999; Koyama, Kato, & Mikami, 2000; Koyama, Kato, Tanaka, & Mikami, 2001; Koyama et al., 1998), and lesions of the ACC impair pain avoidance behaviors in animals (Gabriel, Kubota, Sparenborg, Straube, & Vogt, 1991; LaGraize, Labuda, Rutledge, Jackson, & Fuchs, 2004). Together, these results imply a role for the ACC in the detection and avoidance of aversive stimuli.

2.3. Multisensory modulation of pain

Once nociceptive input reaches the brain, it may interact with other senses that convey information about the body, including touch (Inui, Tsuji, & Kakigi, 2006; Mancini, Nash, Iannetti, & Haggard, 2014; Mouraux & Plaghki, 2007) and vestibular sensation (Ferrè, Bottini, Iannetti, & Haggard, 2013). Additionally, studies showing that noxious stimuli reduce corticospinal excitability indicate a central inhibitory effect of pain on the motor system (Farina, Tinazzi, Le Pera, & Valeriani, 2003; Le Pera et al., 2001). These interactions between pain, innocuous sensation, and motor function may contribute to a multimodal representation of the body that facilitates responses to potentially injurious events (Haggard et al., 2013).

Pain perception can also be modulated by sensory modalities such as vision that are not somatic per se, but may provide a context for pain perception. Viewing the body can reduce the

perceived intensity of a painful stimulus (Longo, Betti, Aglioti, & Haggard, 2009; Longo, Iannetti, Mancini, Driver, & Haggard, 2012; Mancini, Bolognini, Haggard, & Vallar, 2012; Mancini, Longo, Canzoneri, Vallar, & Haggard, 2013) and increase pain detection thresholds (Mancini, Longo, Kammers, & Haggard, 2011) relative to viewing a non-body object in the same location. This visually induced analgesia (Longo et al., 2009) is also apparent in neurophysiological and functional imaging measures. Viewing the body reduced the amplitude of laser-evoked potentials (LEPs) that reflect pain processing (Longo et al., 2009) and altered beta oscillations over sensorimotor cortex (Mancini et al., 2013). Additionally, visually induced analgesia was accompanied by increased functional connectivity between posterior parietal areas that process visual input concerning the body and areas involved in the 'pain matrix', including SI, SII, the anterior and posterior insula, and the ACC (Longo et al., 2012).

While previous studies show that viewing the body can influence pain, several questions remain unanswered. First, it remains unclear whether the changes relate to pain perception specifically, or to other, non-specific post-perceptual cognitive functions. The pain matrix, despite its name, is composed of several nodes that may perform various information processing functions, including functions that are not specific to pain sensation, such as arousal or threat detection (Cauda et al., 2012; Hayes & Northoff, 2012; Iannetti & Mouraux, 2010; Legrain, Iannetti, Plaghki, & Mouraux, 2011; Lötsch et al., 2012; Mouraux, Diukova, Lee, Wise, & Iannetti, 2011). Similarly, some have questioned the validity of LEPs as an index of pain sensation in particular rather than a domain-general measure of stimulus salience (Iannetti, Hughes, Lee, & Mouraux, 2008; Mouraux & Iannetti, 2009). Thus, it is unclear whether viewing the body results in a functional loss of perceptual information in the nociceptive system, or simply changes responses to pain.

2.4. Signal detection theory applied to nociception

Signal detection theory offers a framework for distinguishing between perceptual sensitivity and response bias (Green & Swets, 1966). It is typically applied to a two-alternative forced-choice perceptual task in which the participant must judge on every trial whether a target stimulus near the threshold for detection—for example, a weak vibration against the skin—is present or not.

Regardless of external input to the perceptual system, there is always some baseline variability in neuronal activity, resulting in internal noise. Thus, the internal response of the perceptual system on 'signal present' trials is the sum of the stimulus-evoked signal plus internal noise, whereas the internal response on 'signal absent' trials consists of noise alone. Figure 2.1 shows two normal probability curves representing the distributions of internal responses on 'signal present' and 'signal absent' trials. Perceptual sensitivity is the distance between the means of the 'signal present' and 'signal absent' distributions. In other words, sensitivity refers to the ability of the perceptual system to distinguish stimulus-related signal from noise. Response bias, on the other hand, refers to the internal response level above which the participant will respond that the signal was present, and below which the participant will respond that it was absent. That is, it is the participant's tendency to respond that the target stimulus occurred, irrespective of actual sensory input.

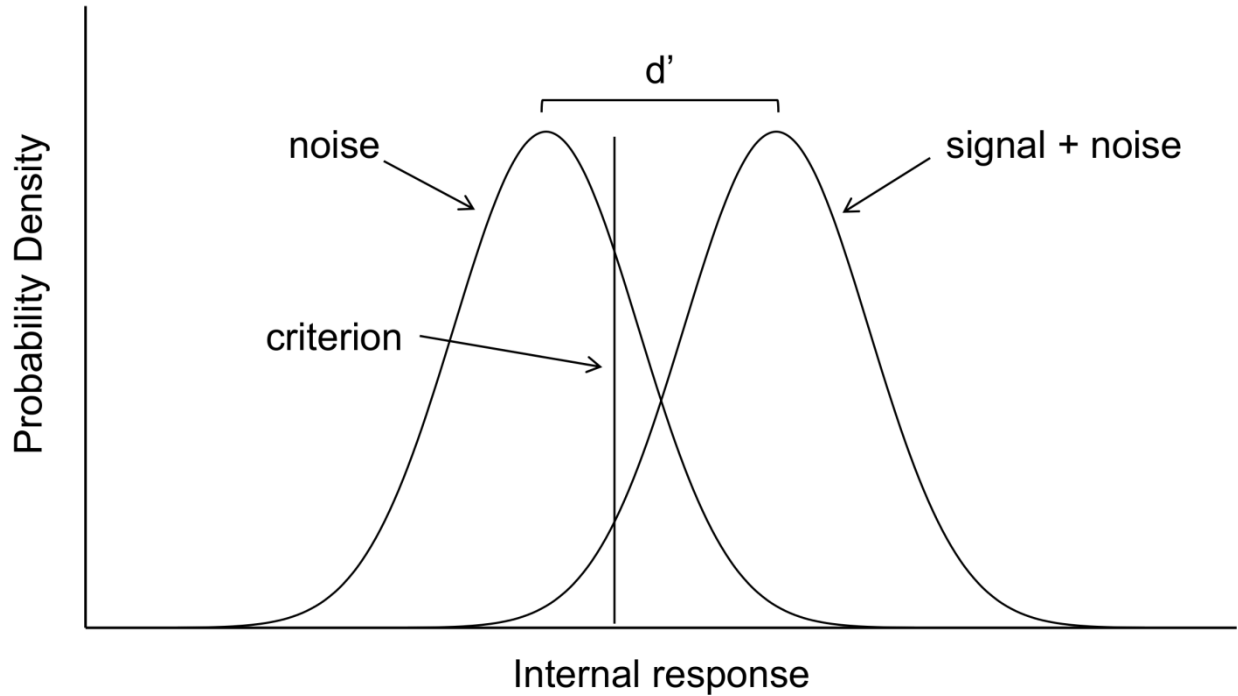


Figure 2.1. A visual representation of the signal detection approach. The two normal probability curves represent the distributions of internal responses on ‘signal present’ and ‘signal absent’ trials. The distance between the means of the distributions is the perceptual sensitivity (d'). The vertical line marks the internal response level above which the participant will report that a signal is present (criterion). Note that the two measures can vary independently. (Adapted from Rollman, 1977.)

In the signal detection approach, rates of hits (correctly reporting that the signal was present) and false alarms (incorrectly reporting that the signal was present when it was absent) are calculated. Measures of perceptual sensitivity (d') and response bias (criterion) are then computed from the z-scores of the hit and false alarm rates, according to the following formulas:

$$d' = z(\text{hit rate}) - z(\text{false alarm rate})$$

$$\text{criterion} = -0.5 * [z(\text{hit rate}) + z(\text{false alarm rate})]$$

A higher d' value indicates greater perceptual sensitivity to the target stimulus. A higher criterion value indicates that a participant requires a larger internal response to report that a signal was present, and will thus make fewer hits and false alarms than another participant with equivalent perceptual sensitivity but a lower criterion. Note that this approach provides additional information beyond other traditional psychophysical measures such as detection rate or detection threshold.

In nociceptive research, the standard signal detection approach may be modified to accommodate the administration of high-intensity stimuli. One approach to this might be to have participants discriminate a level of stimulation just above the pain threshold from another level just below it (Rollman, 1977). However, this approach is not ideal for studying nociception specifically, because it entails discriminating a nociceptive stimulus from an innocuous stimulus processed by a different somatosensory pathway. Rather than reporting whether a stimulus was painful or not, participants can be instructed to discriminate between two levels of noxious stimulation, a higher level and a lower level (Lockwood, Iannetti, & Haggard, 2013; Mancini et al., 2014). In this case, the two normal distributions in Figure 2.1 would represent the internal responses to “lower signal (plus noise)” and “higher signal (plus noise),” and the distance between their means, the d' , would measure the discriminability of the two noxious stimulus levels. The criterion would measure the participant’s tendency to respond “more pain” or “less pain” regardless of the actual stimulation level. This approach was taken in the following three experiments to determine whether viewing the body in various contexts affects the sensitivity of the nociceptive system or biases responses to pain.

Experiment 2: A signal detection approach to studying visual modulation of pain

Experiment 2 aimed to determine whether viewing the body decreases sensitivity to levels of noxious stimulation (i.e., a loss of information about stimulus intensity) or induces a

bias in perceived pain level regardless of the actual intensity of stimulation (i.e., a non-discriminative effect in which the probability of responding “high pain” is changed, irrespective of the actual stimulation level). This distinction was difficult to make in previous studies because pain perception was assessed with continuous pain rating scales (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013) or pain detection thresholds (Mancini et al., 2011). The present study employed binary forced choice pain intensity judgments, making it possible to obtain separate measures of sensory sensitivity and response bias (Lockwood et al., 2013; Mancini et al., 2014). This approach differs from earlier applications of signal detection theory in that it requires participants to discriminate a higher and a lower level of painful stimulation, rather than a painful and a non-painful stimulation level (Rollman, 1977). In this way, it was possible to specifically examine perceptual sensitivity within nociceptive pathways, as opposed to between noxious and non-noxious stimuli. Based on previous studies that found an analgesic effect of viewing the body (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011), it was predicted that viewing one’s own hand compared to viewing a non-body object would decrease the sensitivity of the nociceptive system to noxious intensities (i.e., a reduction in d'), as well as lowering perceived pain levels overall. This would indicate that visually induced analgesia derives from a loss of information about noxious stimulus intensities from viewing the body rather than a post-perceptual bias in responses to painful stimuli.

Method

Participants

Sixteen volunteers participated in the experiment (10 female, 19-42 years old, $M = 26.63$ years, $SD = 8.01$ years). All participants gave written informed consent to participate in the experiment and were treated in accordance with the ethical standards of the 1964 Declaration of

Helsinki. The study was approved by the University College London Research Ethics Committee.

Materials

Contact heat-pain stimuli were delivered with a Peltier thermode connected to a 13-mm diameter pen-shaped probe (Physitemp NTE-2A, Clifton, NJ). A personal computer running Labview 2010 (National Instruments, Austin, TX) and connected to the thermode via a USB-6008 data acquisition device (National Instruments) delivered small voltage levels that controlled the temperature on the metal tip of the thermode probe. The probe was attached to a wood bar controlled by a high-power servo motor (Hitec HS-805BB, Poway, CA) that brought the tip into contact with the hand dorsum. Visual presentation was controlled by a semi-silvered mirror embedded in a barrier with a light-emitting diode (LED) lamp on each side. Participants placed their right hand to the right of the barrier and looked toward it through the mirror in a dark, quiet room. A hand-sized foam block was situated to the left of the mirror, behind another barrier that prevented the participant from seeing it directly. When the lamp on the right side was illuminated, participants saw their right hand through the mirror. When the lamp on the left side was illuminated, participants instead saw the reflection of the foam block, so that it appeared in the same location as their hand (Figure 2.2).

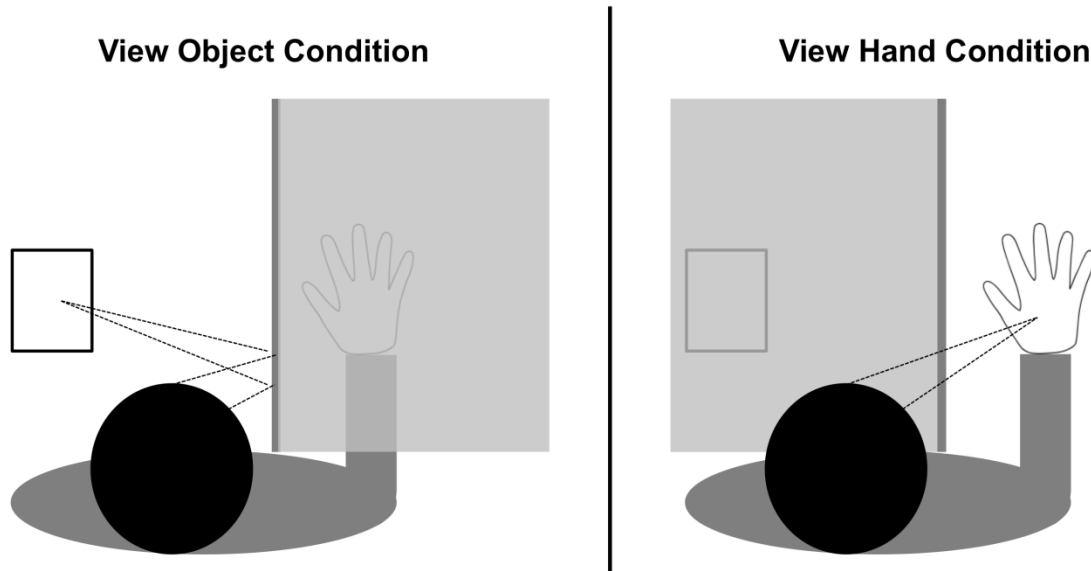


Figure 2.2. Experimental setup with semi-silvered mirror and LED lamps. When the lamp on the right was switched on (right panel), participants saw their own hand through the mirror. Instead, when the lamp on the left was switched on (left panel), participants saw the reflection of the foam block appearing in the same location as their hand.

Procedure

First, each participant's individual pain threshold was determined. The thermode probe was brought into contact with the right hand dorsum. Beginning at 32°C, the probe temperature was increased at a rate of 0.5°C/s until the participant pressed a mouse button with the left hand to indicate that the heat had just begun to elicit a painful, pinprick-like sensation. This temperature ramp was repeated another three times, and the average temperature at which the participant pressed the button was taken as the pain threshold. The right hand was moved slightly between ramps to stimulate a different area of skin. This was necessary to avoid peripheral effects on pain perception such as receptor adaptation, vascular responses, and persistent changes in skin temperature.

Each participant's individual pain threshold was used to set a medium level of heat-pain (a 5% increase in voltage input to the thermode relative to the threshold, corresponding to a temperature increase between 1.5°C and 2°C) and a high level of heat-pain (a 10% increase in voltage relative to the threshold, corresponding to a temperature increase between 3°C and 4°C). Participants then completed two practice blocks of 10 trials each in which they distinguished medium and high heat-pain stimuli. Each thermal stimulus was 1 s long, with a 12-s interval between the offset of one heat-pain stimulus and the onset of the next. Again, the hand was moved slightly between blocks to stimulate a different area of skin. To avoid floor and ceiling effects, the high-pain stimulus intensity was adjusted in increments of 2.5% if participants answered fewer than 65% or more than 85% of trials correctly. Additionally, the medium-pain stimulus intensity was increased by 2.5% if it was not consistently perceived as painful during the practice blocks. For safety reasons, thermal stimulation did not exceed 50°C.

Once the medium-pain and high-pain levels were set, participants completed 8 experimental blocks. Each block contained 6 medium pain trials and 6 high pain trials, presented in a random order and equiprobably with the hand and object visual conditions. On each trial, a lamp switched on for 2 s, revealing either the participant's hand or the foam block. Immediately after the lamp switched off, the thermode probe descended (0.5 s), touched the back of the hand (1 s), and then retracted (0.5 s). Note that participants did not see the thermode probe approach or contact their hand. Participants pressed a button on a mouse in their left hand to indicate whether they felt a medium-pain or a high-pain stimulus. To minimize peripheral effects on pain perception, the hand was moved slightly between blocks, and there was an interval of 9 s between trials.

Results

The high-pain level was defined as the target stimulus. A 'hit' was thus a high-pain stimulus correctly identified as high-pain, while a 'false alarm' was a medium-pain stimulus incorrectly identified as high-pain. The proportions of hits and false alarms were used to calculate measures of sensitivity (d') and response bias (criterion) according to the formulas given above (Green & Swets, 1966). Note that if the medium-pain level had been selected as the target stimulus instead, the calculations would yield the same d' values, and the criterion values would just reverse their sign.

Paired-samples t-tests compared d' and criterion scores in the hand and object visual conditions. Sensitivity to noxious heat intensities (d') was lower after participants saw their hand ($M = 1.35$, $SEM = \pm 0.15$) than after they saw the object ($M = 1.66$, $SEM = \pm 0.18$), $t(15) = 2.24$, $p = .041$. There was no difference in criterion between hand ($M = -0.01$, $SEM = \pm 0.07$) and object ($M = 0.09$, $SEM = \pm 0.10$) visual conditions, $t(15) = 1.22$, $p = .243$. This indicates that viewing the body reduced the discriminability of noxious stimulation levels rather than biasing pain responses (Figure 2.3A).

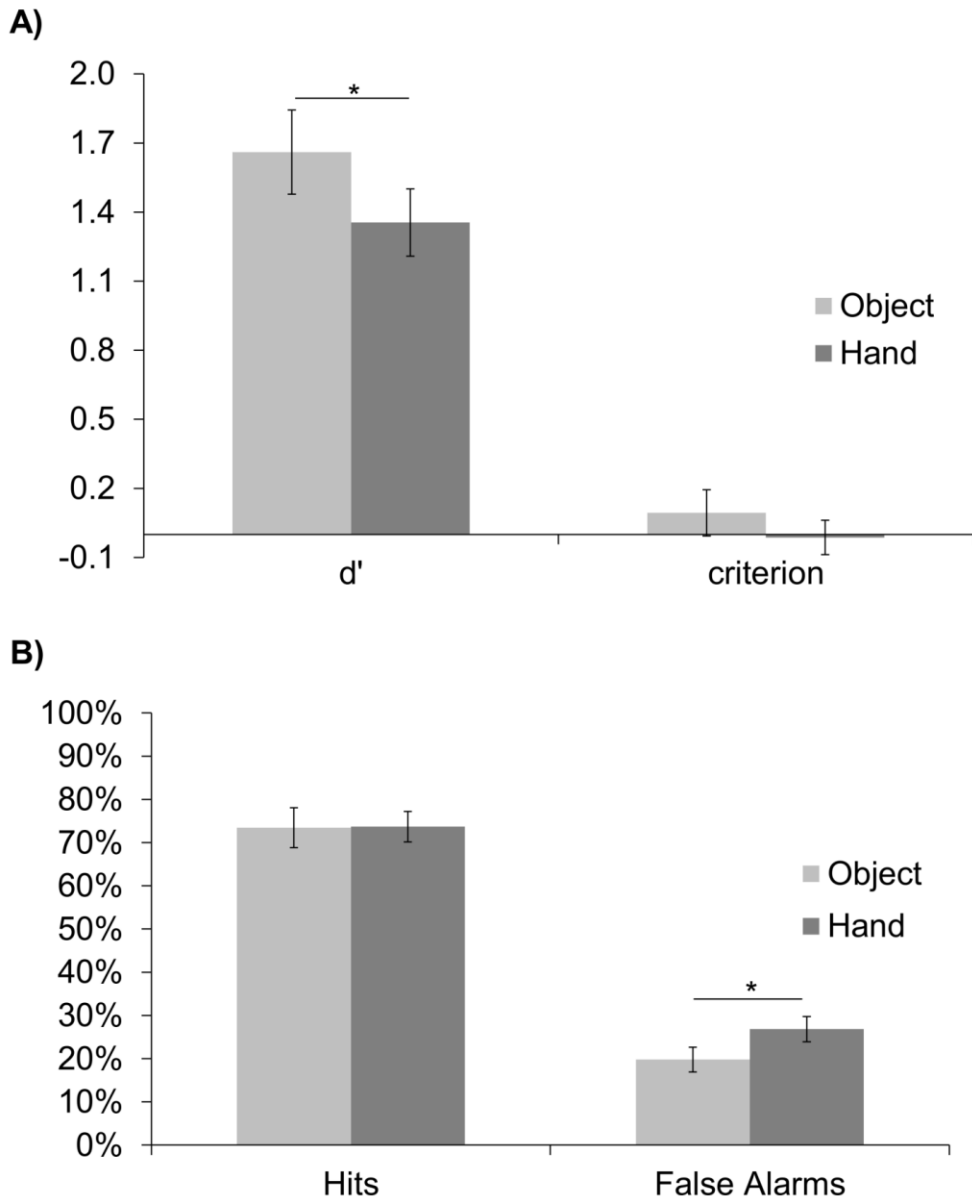


Figure 2.3. Results of Experiment 2. Participants saw either their hand or the object in a randomized order, and then felt a noxious heat stimulus in darkness. A) Mean (\pm SEM) scores of perceptual sensitivity (d') and response bias (criterion) to noxious heat after viewing the hand and the object. B) Mean (\pm SEM) rates of hits (high pain stimuli called high pain) and false alarms (medium pain stimuli called high pain) after viewing the hand and the object. * = $p < .050$.

To see whether the reduction in sensitivity after viewing the hand produced an overall analgesic effect, as previous studies have found (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011), two additional paired-samples t-tests compared proportions of hits and false alarms after participants viewed the hand and the foam block. Because the target stimulus was the high-pain level, a lower hit rate would indicate a decrease in perceived pain intensity. In fact, there was no difference in the hit rate between the hand ($M = 73.70\%$, $SEM = \pm 3.52\%$) and the object ($M = 73.44\%$, $SEM = \pm 4.63\%$) conditions, $t(15) = -0.08$, $p = .936$. Instead, participants made more false alarms after viewing their hand ($M = 26.82\%$, $SEM = \pm 2.90\%$) than after viewing the object ($M = 19.79\%$, $SEM = \pm 2.86\%$), $t(15) = -2.30$, $p = .036$, meaning that more medium-pain stimuli were perceived as high-pain stimuli following vision of the hand. In contrast to previous studies, viewing the hand yielded an *increase* in perceived pain intensity at lower levels of noxious stimulation (Figure 2.3B).

Discussion

Experiment 2 demonstrated that viewing the body modulates pain perception at a perceptual level, rendering intensities of noxious stimulation less discriminable. There was no visual modulation of bias in pain responding. Surprisingly, this reduced sensitivity to differences in noxious stimulus intensity resulted in more medium-pain stimuli being perceived as high-pain stimuli. Previous studies in which participants reported the intensity of painful stimuli on a continuous rating scale (from 0-100) instead found that viewing the body decreases overall perceived pain intensity (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013). Similarly, Mancini and colleagues (2011) found an increase in pain detection thresholds when participants viewed their hand. They used a gradually increasing contact-heat ramp and instructed their participants to press a button as soon as the heat began to feel painful (akin to the method used in Experiment 2 to find each participant's pain threshold). These methods differ from that of the present experiment in that they do not require participants to

discriminate different intensities of noxious stimulation. Thus, the difference in the direction of the effect found in the present study might be due to the type of task used, namely noxious stimulus intensity discrimination rather than pain intensity magnitude estimation (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013) or pain detection (Mancini et al., 2011).

Alternatively, differences in visual stimulation between Experiment 2 and the previous studies might account for the discrepant findings. The earlier studies (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011) presented the hand and object visual conditions in separate blocks (with the exception of the second experiment reported by Mancini et al., 2013, which yielded a still-significant but markedly smaller reduction in perceived pain intensity when viewing the hand). In Experiment 2, the hand and object visual conditions varied randomly on a trial-by-trial basis. Compared to prior studies, visual exposure was brief and its content was unpredictable, which might alter its implications for pain perception. Indeed, studies on pain expectation have found that perception of noxious stimuli is affected by predictability, with predictable painful stimuli typically being perceived as less intense than physically identical but unpredictable painful stimuli (Carlsson et al., 2006; Crombez, Baeyens, & Eelen, 1994; Meulders, Vansteenwegen, & Vlaeyen, 2012). These effects may generalize beyond the predictability of the painful stimulus of interest to the context in which it is presented (Rhudy & Meagher, 2000). Experiment 3 tested this hypothesis by presenting blocks in which participants saw only the hand or the object, thus making the content of visual stimulation entirely predictable and consistent over time.

Experiment 3: The effect of visual stimulus predictability on visual modulation of pain

Method

Participants

Sixteen different volunteers participated in the experiment (6 female, 18-53 years old, $M = 27.31$ years, $SD = 8.92$ years). Two participants were dismissed during pain threshold determination and subsequently replaced because they did not perceive even the highest level of thermal stimulation as painful. All participants gave written informed consent to participate in the experiment and were treated in accordance with the ethical standards of the 1964 Declaration of Helsinki. The study was approved by the University College London Research Ethics Committee.

Materials and Procedure

The materials and procedure of Experiment 3 were exactly the same as those of Experiment 2, except that participants saw their hand on every trial in 4 of the blocks and the foam block on every trial in the other 4 blocks. Block order was counterbalanced across participants (HHOOHHOO for half the participants, and OOHOOHH for the other half). Once again, the thermode probe approached and touched the hand in darkness, so participants did not see the pain-inducing event.

Results

As in Experiment 2, the high pain level was defined as the target stimulus, and the proportions of hits and false alarms were used to calculate measures of sensitivity (d') and response bias (criterion). One participant did not have any false alarms in the hand visual condition, so a standard correction was applied to estimate the false alarm rate (Macmillan &

Kaplan, 1985). Specifically, the false alarm rate was set to $1/(2N)$, where N is the maximum number of false alarms the participant could make (i.e., the total number of medium-pain trials in the hand visual condition). This yields a false alarm rate halfway between 0 and the smallest false alarm rate the participant could have had, given the number of medium-pain trials.

Mixed factor analyses of variance (ANOVAs) with the within-subjects factor 'visual condition' (hand or object) and the between-subjects factor 'experiment' (Exp 2: randomized visual presentation, or Exp 3: blocked visual presentation) were carried out on d' and criterion scores. There was a trend toward lower d' scores after viewing the hand ($M = 1.25$, $SEM = \pm 0.12$) than after viewing the object ($M = 1.44$, $SEM = \pm 0.14$) regardless of whether they were presented in the same or different blocks, $F(1, 30) = 3.26$, $p = .081$, partial $\eta^2 = .098$. There was also a significant main effect of visual condition on criterion scores, $F(1, 30) = 5.78$, $p = .023$ partial $\eta^2 = .161$. Criterion was lower after viewing the hand ($M = -0.01$, $SEM = \pm 0.08$) than after viewing the object ($M = 0.13$, $SEM = \pm 0.07$), meaning that participants were more likely to respond 'high pain' after seeing their hand irrespective of the actual intensity of the noxious stimulus.

Comparisons between Experiments 2 and 3 showed no main effects of experiment (d' : $p = .188$; criterion: $p = .793$), nor interactions between experiment and visual condition (d' : $p = .310$; criterion: $p = .552$). However, visual inspection of the data suggests that the effect of viewing the body on sensitivity was stronger when visual presentation was randomized, whereas the effect on criterion seemed to predominate when presentation was blocked (Figure 2.4A).

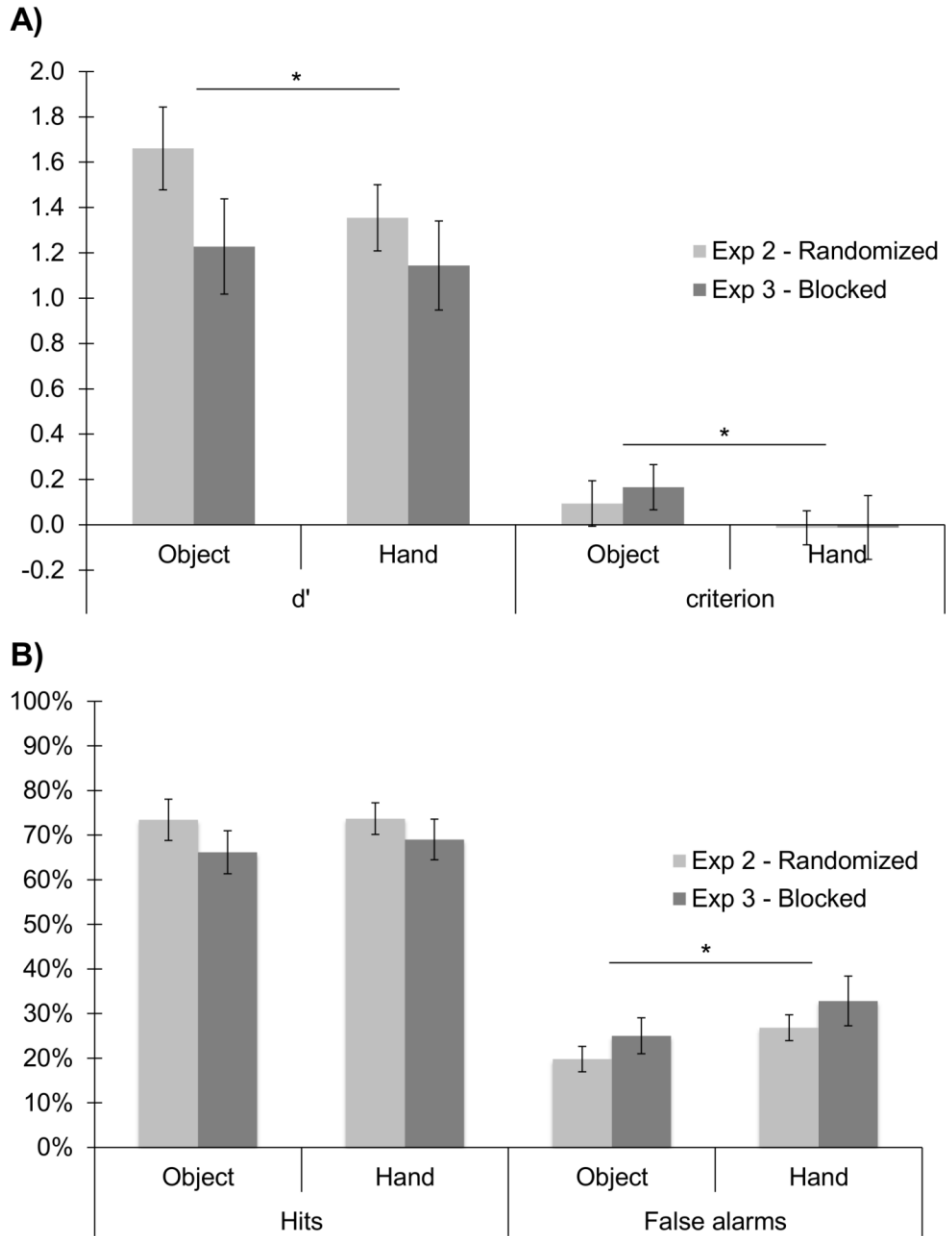


Figure 2.4. Combined results of Experiments 2 and 3. Participants saw their hand and the object in a randomized order (Exp 2) or a blocked order (Exp 3), and then felt a noxious heat stimulus in darkness. A) Mean (\pm SEM) scores of perceptual sensitivity (d') and response bias (criterion) to noxious heat after viewing the hand and the object. B) Mean (\pm SEM) rates of hits (high pain stimuli called high pain) and false alarms (medium pain stimuli called high pain) after viewing the hand and the object. * = $p < .050$ (main effects of visual condition).

Mixed factors ANOVAs on hit and false alarm rates confirmed the results of Experiment 2 alone. There was a main effect of visual condition on the false alarm rate, $F(1, 30) = 10.91$, $p = .002$, partial $\eta^2 = .267$. Participants perceived more medium-pain stimuli as high-pain stimuli after viewing the hand ($M = 29.82\%$, $SEM = \pm 3.14\%$) than after viewing the object ($M = 22.40\%$, $SEM = \pm 2.47\%$) regardless of whether visual presentation was randomized or blocked. There was no main effect of experiment (randomized vs. blocked presentation), $F(1, 30) = 1.17$, $p = .289$, partial $\eta^2 = .037$, and no interaction between experiment and visual condition, $F(1, 30) = 0.03$, $p = .863$, partial $\eta^2 = .001$. The hit rate analysis found neither a main effect of visual condition, $F(1, 30) = 0.43$, $p = 0.515$, partial $\eta^2 = .014$, nor of experiment, $F(1, 30) = 1.08$, $p = .308$, partial $\eta^2 = .035$. Moreover, there was no interaction between the two factors, $F(1, 30) = 0.30$, $p = .587$, partial $\eta^2 = .010$ (Figure 2.4B).

Discussion

In Experiment 2, viewing the body yielded a functional loss of information about noxious stimulus intensities. The analysis of Experiments 2 and 3 together extends these findings. In addition to the reduction in sensitivity, participants were biased toward reporting a higher level of pain after viewing their hand than after viewing the non-body object, regardless of the actual intensity of the heat-pain stimulus. This indicates two potential mechanisms whereby viewing the body might influence pain perception. First, viewing the body appears to have an effect at the sensory level of nociception, reducing the discriminability of noxious stimulation intensities. Second, vision of the hand also biases participants' criterion for what is painful, in this case leading them to report higher pain levels, irrespective of stimulation intensity. Finally, it can be concluded that the unpredictability of visual stimulation in Experiment 2 was not responsible for participants perceiving more medium-pain stimuli as high-pain stimuli after viewing their hand, because this effect was also present in Experiment 3.

Because there were no interactions between experiment and visual condition, the effects of viewing the body on sensitivity and response bias manifested to some extent both when the order of hand and object presentation was randomized (Experiment 2) and when the two were presented in separate blocks (Experiment 3). Nevertheless, the reduction in sensitivity seemed to be stronger in Experiment 2. This effect only reached the level of a trend in the combined analysis of Experiments 2 and 3, although a one-tailed test would be warranted given the prediction of a visually-induced reduction in sensitivity. Conversely, response bias seemed to predominate in Experiment 3 (Figure 2.4B). A difference in the predictability of visual stimulation might alter the balance between the effects of viewing the body on sensitivity and response bias, with the more stable visual context favoring a bias effect.

While several studies have previously investigated the effects of viewing the body on pain perception, the precise visual stimulus used varies dramatically. For example, studies have involved viewing one's own hand (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011), another's hand (Longo et al., 2009), or another's hand perceived as one's own hand (Höfle, Hauck, Engel, & Senkowski, 2012; Höfle, Pomper, Hauck, Engel, & Senkowski, 2013). In addition, some studies involved viewing the pain-inducing event in addition to the body (Höfle et al., 2012, 2013; Mancini et al., 2013). Viewing the body and viewing noxious stimulation on the body might potentially have quite different effects on pain perception. Moreover, these effects might interact. For instance, viewing an image of a needle pricking a hand increased ratings of the intensity and unpleasantness of a painful intracutaneous electrical stimulus, which elicits a pinprick-like sensation (Höfle et al., 2012, 2013). In another study, however, participants saw a thermode probe approach and deliver a painful heat stimulus to either their hand or a non-body object, and gave lower pain intensity ratings when viewing the probe touch their hand (Mancini et al., 2013). Thus, there is contradictory evidence for whether viewing a threatening stimulus approach the body has a

similar effect on pain perception as viewing the body alone. Experiment 4 aimed to systematically compare these two conditions and their effects on both sensitivity to noxious stimulus intensities and bias in perceived pain level.

Experiment 4: The effect of viewing the pain-inducing event on pain perception

Method

Participants

Sixteen additional volunteers were recruited for Experiment 4 (10 female, 19-36 years old, $M = 23.81$ years, $SD = 5.08$ years). One was dismissed during pain threshold determination and subsequently replaced because he did not perceive even the highest level of thermal stimulation as painful. All participants gave written informed consent to participate in the experiment and were treated in accordance with the ethical standards of the 1964 Declaration of Helsinki. The study was approved by the University College London Research Ethics Committee.

Materials and Procedure

The materials and procedure of Experiment 4 were the same as those of Experiment 2, except that the timing of visual stimulation was shifted to coincide with the delivery of heat-pain stimulation. A second, inactive thermode probe was attached to another motor-controlled wood bar over the block and moved synchronously with the probe over the participant's hand. On each trial, either the hand or the foam block was illuminated as the thermode probe began to descend, so that the participant saw the probe approach and contact the hand or the block. The order of hand and object presentation was randomized, as in Experiment 2, and trial and block durations were the same as in the previous experiments. Thus, Experiment 4 recapitulated Experiment 2 with the additional factor of viewing the approaching noxious stimulation.

Results

Once again, the high-pain level was defined as the target stimulus, and the proportions of hits and false alarms were used to calculate measures of sensitivity (d') and response bias (criterion). As in Experiment 3, one participant did not have any false alarms in the hand visual condition, so a standard correction was applied to estimate the false alarm rate (Macmillan & Kaplan, 1985). Mixed factor ANOVAs with the within-subjects factor 'visual condition' (hand or object) and the between-subjects factor 'experiment' (Exp 4: thermode probe approach visible, or Exp 2: thermode probe approach not visible) were carried out on d' scores, criterion scores, hit rates, and false alarm rates. For sensitivity (d'), there was an interaction between the two factors, $F(1, 30) = 6.24, p = .018, \text{partial } \eta^2 = .172$. In Experiment 2, when noxious stimulation was delivered in darkness, participants were less able to discriminate the two heat-pain stimulation intensities when they viewed their hand ($M = 1.35, SEM = \pm 0.15$) than when they viewed the object ($M = 1.66, SEM = \pm 0.18$), $t(15) = 2.24, p = .041$. In contrast, when participants saw the thermode probe approach and deliver the painful stimulus in Experiment 4, there was an increase in sensitivity to heat-pain intensities when viewing the hand ($M = 1.26, SEM = \pm 0.16$) compared to viewing the object ($M = 1.09, SEM = \pm 0.17$). This increase, however, was not statistically significant, $t(15) = -1.26, p = .226$ (Figure 2.5A). Pairwise comparisons between experiments revealed lower sensitivity when viewing the probe touch the object in Experiment 4 than when viewing the object alone in Experiment 2, $t(30) = 2.30, p = .029$. There was no difference in sensitivity between viewing the probe touch the hand and viewing the hand alone, $t(30) = 0.47, p = .644$.

There was no main effect of visual condition on d' ($p = .441$), criterion ($p = .106$), hit rates ($p = .206$), or false alarm rates ($p = .096$). There was also no main effect of experiment on any of these measures (d' : $p = .124$, criterion: $p = .704$; hits: $p = .232$; false alarms: $p = .255$). Finally, there was no interaction between visual condition and experiment for criterion ($p =$

.946), hits ($p = .245$), or false alarms ($p = .149$). Mean scores in each condition are shown in Figure 2.5.

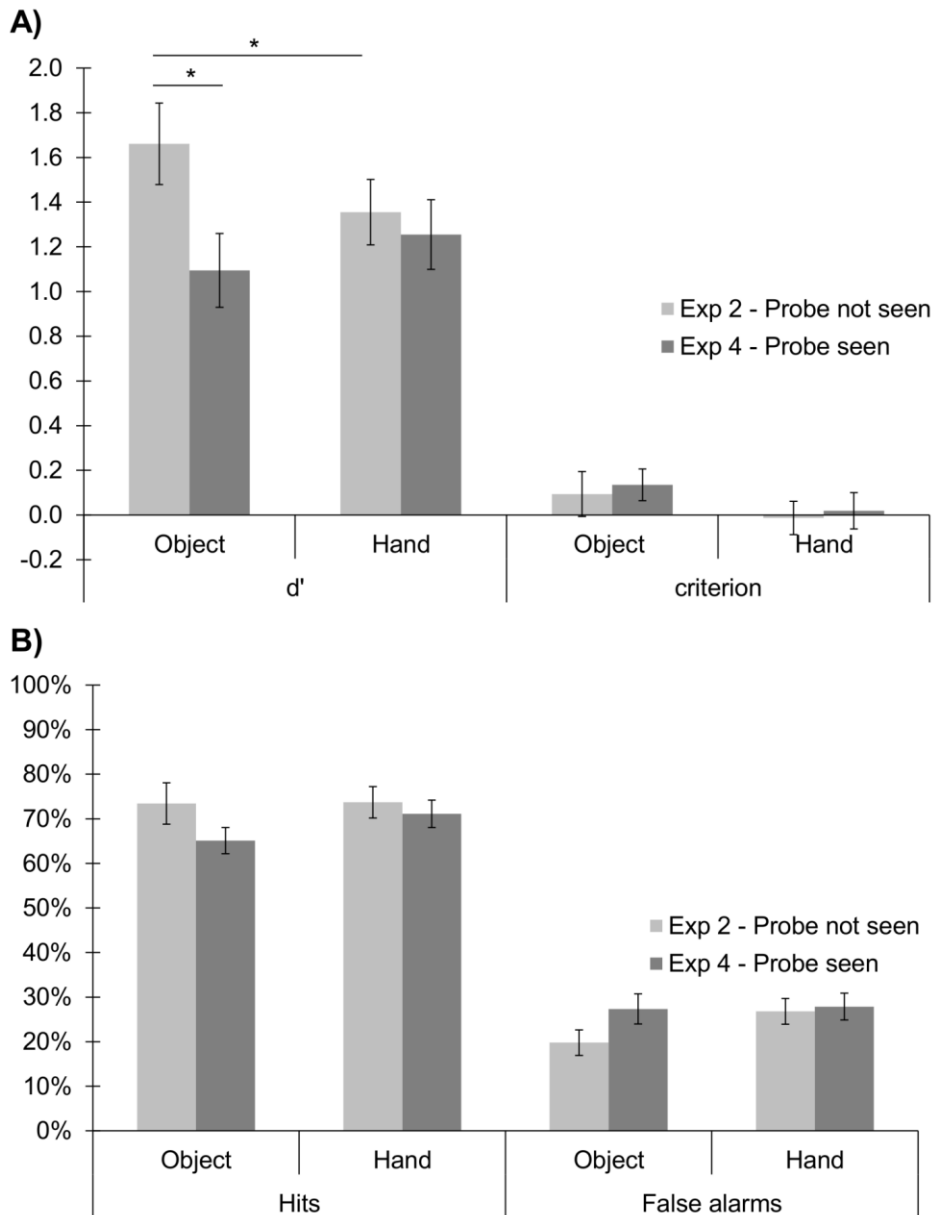


Figure 2.5. Combined results of Experiments 2 and 4. Participants either saw their hand or the object before feeling a noxious heat stimulus in darkness (Exp 2), or they saw the thermode probe approach and touch their hand or the block while feeling the noxious heat stimulus (Exp

4). A) Mean (\pm SEM) scores of perceptual sensitivity (d') and response bias (criterion) to noxious heat when viewing the hand and the object. B) Mean (\pm SEM) rates of hits (high pain stimuli called high pain) and false alarms (medium pain stimuli called high pain) when viewing the hand and the object. * = $p < .050$.

Discussion

The key difference between Experiments 2 and 4 was whether participants did or did not see the thermode probe while receiving the heat-pain stimulus. A between-experiments analysis revealed that the reduction in sensitivity to noxious stimulation intensities after viewing the hand was eliminated when participants saw the probe deliver the noxious stimulus. In fact, there was a non-significant trend in the opposite direction, with higher d' scores when viewing the hand being touched by the probe than when viewing the block being touched.

Importantly, seeing the thermode probe approach in Experiment 4 did not provide any additional information about the occurrence, timing, or strength of the thermal stimulus. Participants were aware that they would feel a heat-pain stimulus on every trial, regardless of whether they saw their hand or the foam block. Moreover, the heat-pain stimulus was delivered at the same time on every trial in both experiments, and was completely predictable from the offset of the LED lamp in Experiment 2. Therefore, the difference between Experiment 4 and Experiment 2 is not in the predictability of the noxious stimulus, but in actually seeing the thermode probe come into contact with the body or the non-body object.

General Discussion: Experiments 2-4

I. Viewing the body modulates both pain sensations and pain responses

Experiment 2 clearly showed that viewing the body reduced sensitivity to differences in noxious heat intensity. Participants were less able to discriminate the medium and high heat-pain stimuli after viewing their hand than after viewing the foam block appearing in the same location as their hand. This indicates a functional loss of information about stimulus intensity from the nociceptive system as a result of viewing the body, independent of any effect of spatial attention. Building on prior research (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011), this experiment demonstrates that viewing the body does not merely reduce reported pain level, but inhibits the sensory processing responsible for encoding nociceptive stimulus intensity, rendering variations in the level of noxious stimulation less discriminable.

The comparison between Experiments 2 and 3 revealed that viewing the body can also bias perceived pain level irrespective of actual stimulus intensity. Interestingly, the direction of this bias was opposite to the effect found in previous studies that found visually induced analgesia (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011). Participants in Experiments 2 and 3 tended to report higher levels of pain after viewing the hand. In particular, they perceived more medium-pain stimuli as high-pain stimuli following vision of the hand compared to vision of the non-body object. As discussed earlier, the difference in the direction of the effect on perceived pain level might be due to the kind of task used. Experiments 2, 3, and 4 used a binary forced choice discrimination task, whereas previous studies used pain detection thresholds (Mancini et al., 2011) or continuous pain rating scales (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013). Differences between the kinds of pain judgments made in these tasks could account for the

apparent discrepancy in the direction of the modulation. A loss of noxious intensity information from the nociceptive system could lead to lower intensity ratings in a magnitude estimation task. Instead, in a forced choice discrimination task, it might lead participants to identify more noxious stimuli as 'high pain' because the stimuli feel less intense overall, so participants may adjust their concept of 'high pain' to include lower perceived intensity levels.

Additionally, the duration of visual stimulation might be an important difference between the present studies and previous studies on visual modulation of pain perception. In Experiments 2 and 3, participants had brief, 2 s glimpses of their hand or the foam block that preceded contact heat pain stimulation. In the previous studies, vision of the hand/object lasted at least 5 s, and it both preceded and overlapped with the timing of the noxious stimulus. Either the absolute duration of visual stimulation or the relative onset of the visual stimulus relative to the noxious stimulus might affect visual modulation of pain perception. A systematic investigation of these factors should be done in future studies.

One might argue that the experimental procedures used to investigate visual modulation of pain find an effect of viewing the body because they cause a multisensory conflict, that is, the sensation of a noxious stimulus on the hand without a visible pain-inducing stimulus. Previous authors have refuted this claim by demonstrating that visual modulation of pain perception can occur even when participants view their hand directly and see the pain-inducing stimulus on their hand (Longo et al., 2009; Mancini et al., 2013) or when a 'dummy stimulus' gives the impression that the pain-inducing stimulus is visible (Mancini et al., 2011). For the present study, it is important to note that none of the experiments caused a visuo-somatosensory conflict. In Experiments 2 and 3, the noxious stimulus was administered in total darkness, following vision of the hand or the block. In Experiment 4, participants saw the thermode probe approach and contact their hand (or the foam block, which appeared in the same location). Therefore, multisensory conflict cannot explain the results.

II. A neural mechanism for visual modulation of nociception

Previous studies suggest that visual modulation of pain perception occurs via functional connections from visual body processing areas in the extrastriate and posterior parietal cortices to areas of the pain matrix, including SI, SII, the insula, and the ACC (Longo et al., 2012; Mancini, Bolognini, et al., 2012). The results of the present study, particularly Experiment 2, indicate that vision of the body modulates activity in a region responsible for encoding sensory/discriminative aspects of nociception. Though several nodes of the pain matrix have been implicated in processing sensory/discriminative aspects of pain (Bornhövd et al., 2002; Büchel et al., 2002; Frot, Magnin, Mauguière, & Garcia-Larrea, 2007; Hofbauer, Rainville, Duncan, & Bushnell, 2001; Iannetti, Zambreanu, Cruccu, & Tracey, 2005; Kong et al., 2006; Ohara, Crone, Weiss, Treede, & Lenz, 2004; Peyron, Laurent, & Garcia-Larrea, 2000; Timmermann et al., 2001), some have proposed that the operculo-insular cortex has a primary role in encoding noxious stimulus intensity (Garcia-Larrea, 2012; Garcia-Larrea, 2012; Mazzola, Faillenot, Barral, Mauguière, & Peyron, 2012). In support of this claim, single pulses of transcranial magnetic stimulation (TMS) over SII, but not SI, reduced discrimination accuracy and d' scores in a binary forced choice pain intensity discrimination task like the one used in Experiments 2, 3, and 4 (Lockwood et al., 2013). Another study found that the N1 component of the laser-evoked potential—localized to the operculo-insular cortex by a source analysis—showed the shortest peak latency and the largest enhancement during a similar heat-pain intensity discrimination task (Schlereth, Baumgärtner, Magerl, Stoeter, & Treede, 2003). These studies suggest that viewing the body may reduce sensitivity to noxious heat intensities through a modulatory effect of the visual body network on nociceptive circuits in the operculo-insular region.

Alternatively, the reduction in nociceptive sensitivity produced by viewing the body may result from modulation of SI. At least one study found the pattern of neurophysiological activity

in SI to be more consistent with pain intensity processing than the activity in SII (Timmermann et al., 2001). Moreover, responses of nociceptive neurons in monkey SI correlate with the monkey's response time to small changes in noxious heat intensity (Kenshalo, Jr. et al., 1988). Some forms of chronic pain are associated with disinhibition of the primary motor and somatosensory cortices (Eisenberg et al., 2005; Lefaucheur et al., 2006; Lenz et al., 2011; Schwenkreis et al., 2003) and with disorganization of SI somatotopic maps (Flor et al., 1995; Flor et al., 1997; Maihöfner et al., 2003; Tecchio et al., 2002; Wrigley et al., 2009). Modulation of SI somatotopy is therefore another possible mechanism by which viewing the body might affect the processing of pain intensity.

III. Viewing the body under threat

Experiment 4 showed that sensitivity to noxious heat intensities is not reduced by vision of the body when the pain-inducing event is also visible. Vision of the body being touched actually yielded higher d' scores than vision of the foam block being touched, though this difference was not statistically significant. Outside the laboratory, acute pain is generally associated with a visible external event or object, making this the most naturalistic of the three pain experiments. Thus, while viewing the body might reduce nociceptive sensitivity under certain experimental conditions, this reduction may not occur very often under normal, everyday circumstances. The comparison between Experiment 2 and Experiment 4 suggests a clear dissociation between effects of seeing the body and effects of seeing noxious stimulation. Some previous studies have amalgamated these two distinct yet interacting effects under the single general concept of 'seeing touch'. The results of these experiments highlight the need to distinguish between them.

One possible reason that nociceptive sensitivity was not reduced when viewing the hand in Experiment 4 could be that seeing the approach of a potentially harmful object in peripersonal

space actually enhances sensitivity to pain intensity, and this counteracts the effect of seeing the body itself. Indeed, this enhancement could serve an adaptive value in helping the observer identify and avoid threats to body integrity. Previous studies have found that viewing an image of a needle pricking a hand over one's own hand increases intensity and unpleasantness ratings of concurrently administered painful stimuli (Höfle et al., 2012, 2013). The results of Experiment 4 hint that viewing a threatening stimulus approach the body might also boost sensory/discriminative aspects of nociception. However, this explanation is weakened by the observation that sensitivity was lower when viewing the foam block being touched in Experiment 4 relative to viewing the block alone in Experiment 2.

An alternative explanation could be that viewing the foam block being touched by the probe while being touched on one's own hand caused the block to be 'embodied', as in the rubber hand illusion (Botvinick & Cohen, 1998). This might have resulted in vision of the foam block having an effect similar to vision of the hand. Objects that do not resemble body parts are not usually embodied (Tsakiris et al., 2010, 2008; Tsakiris & Haggard, 2005; but see Armel & Ramachandran, 2003). Nevertheless, the salience of painful stimulation might yield a lower criterion for embodiment of a foreign object than the typical embodiment paradigm, which combines visual information and innocuous touch. In Experiment 4, the appearance of touch on the foam block consistently co-occurred with a painful stimulus on the participant's own hand, in a way that only the appearance of touch on one's own hand normally would. The adaptive value of learning this correspondence may have outweighed the visual evidence against the foam block being a body part. It is not possible to form a conclusion about this from Experiment 4, as embodiment was not measured. However, another study found an enhancement of the rubber hand illusion when painful tactile stimulation was used rather than innocuous tactile stimulation (Capelari et al., 2009), suggesting that noxious stimulation might in fact strengthen the propensity to embody an external object.

IV. Viewing the body: An attentional effect?

One might contend that the effect of viewing the body on pain perception is simply an effect of attention. However, a purely attentional account cannot explain all of the results. First, it is not clear whether viewing the hand or the object would attract more attentional resources. The hand might be a more interesting visual stimulus than the foam block. Alternatively, seeing the block in the location of one's hand might increase attention because of the visuo-proprioceptive incongruency. Because heightened attention tends to both increase pain ratings (Arntz, Dreessen, & Merckelbach, 1991; Hodes, Rowland, Lightfoot, & Cleeland, 1990; Levine, Gordon, Smith, & Fields, 1982; Miron, Duncan, & Bushnell, 1989) and improve detection of changes in noxious stimulus intensity (Bushnell, Duncan, Dubner, Jones, & Maixner, 1985; Miron et al., 1989), the data do not provide clear evidence for one visual condition being more attention-grabbing than the other. After viewing the hand, participants tended to report higher levels of pain, but they were also less sensitive to differences in heat-pain intensity.

Second, in Experiments 2 and 3, visual stimulation occurred prior to heat-pain stimulation. It is unlikely that any difference in attention to the visual stimulus would have an effect on perception of the noxious stimulus, as they were presented at separate, non-overlapping time periods. Furthermore, in Experiments 2 and 3, the noxious stimulus was delivered in a dark and quiet environment. Though the possibility of distraction cannot be completely ruled out, these conditions should have promoted the full direction of attention toward the task-relevant noxious stimulus, regardless of the visual condition that preceded it.

V. Conclusion

Together, the results of Experiments 2, 3, and 4 indicate that viewing the body can have two distinct effects on pain perception. First, viewing the body reduces the sensitivity of the nociceptive system to differences in the level of noxious stimulation. Second, viewing the body

can bias perceived pain level regardless of actual stimulus intensity. Though these two effects may co-occur, the former seems more pronounced when vision of the body is brief and unpredictable, whereas the latter tends to predominate when the visual body context is predictable and consistent over time. Lastly, viewing the pain-inducing event seems to counteract the reduction in nociceptive sensitivity. However, it is not clear whether this is due to a generalizable effect of seeing a threatening object approach in peripersonal space, or to embodiment of the non-body object as a result of the correlated visual and tactile/nociceptive inputs in the experiment.

For the most part, the first two chapters have dealt with the somatosensory consequences of viewing the body when vision is non-informative about any noxious or innocuous tactile stimulation. The results of Experiment 4 make it clear that viewing a somatosensory event on the body may have effects distinct from those of viewing the body alone. The next chapter will discuss the effect of viewing the body being touched on tactile perception. In particular, it will examine the consequences of viewing touch on the face, a body part that is especially important for both identity and emotion recognition.

Chapter 3: Visual remapping of touch on the face

3.1. Face perception

The face holds a special place in the representation of the human body. It is one of our most salient cues for identifying others. Face perception provides us with information about the other person's age, gender, familial relationships, and ethnic background. If the person is familiar to us, we can recall stored knowledge and previous experiences that may facilitate social interactions with the person. Likewise, our own face is an important part of our self-identity. Faces also serve as powerful communicative tools. As well as being the conduit for verbal communication, faces send many non-verbal cues through eye gaze and, in particular, facial expressions. Facial expressions are the primary way through which we express emotions. They can alert others to the presence of a threat, invite further positive interaction, and signal a wide variety of other cues to those around us.

Models of face perception tend to subdivide it into two general domains: facial identity perception and facial expression perception (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000). The former would require representations of invariant, structural properties of individual faces, as well as links to higher-order, person-specific semantic information and episodic memories. The latter comprises the perception of dynamic facial cues such as gaze direction and muscle configurations, with connections to emotion recognition and communicative functions. There is evidence to suggest that the mechanisms for perceiving facial identity and facial expressions are at least partially distinct. Patients with prosopagnosia are impaired at recognizing identity from faces, but often exhibit spared facial expression recognition (Duchaine, Parker, & Nakayama, 2003; Humphreys, Avidan, & Behrmann, 2007; Sergent & Villemure, 1989; Tranel, Damasio, & Damasio, 1988). Neurophysiological (Bobes, Martín, Olivares, & Valdés-Sosa, 2000; Eimer & Holmes, 2002) and imaging studies (Sergent, Ohta, Macdonald, &

Zuck, 1994; Winston, Henson, Fine-Goulden, & Dolan, 2004) have also provided evidence for segregated processing of facial identity and expressions in healthy participants. However, other studies suggest that facial identity and facial expression mechanisms interact, with a particular influence of facial identity on facial expression recognition (Calder & Young, 2005; Ellamil et al., 2008; Fox & Barton, 2007; Fox et al., 2008; Schweinberger & Soukup, 1998; Spangler et al., 2010).

Studies on the neural basis of face perception have found two areas in the extrastriate occipito-temporal cortex that respond selectively to the sight of human faces: the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) and the occipital face area (OFA) (Gauthier et al., 2000). The OFA appears to be more selective for individual parts of the face, whereas the FFA shows a greater response to viewing the face as a whole (Liu, Harris, & Kanwisher, 2010; Nichols, Betts, & Wilson, 2010; Pitcher, Walsh, Yovel, & Duchaine, 2007; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). Interestingly, this parallels the functions of the nearby EBA and FBA in visual body perception, with the EBA showing greater selectivity for body parts and the FBA responding preferentially to whole-body stimuli (Taylor et al., 2007). Various models of face perception have proposed that the OFA performs a low-level structural encoding of face stimuli, whereas the FFA is involved in higher-level, configural aspects of face processing (Calder & Young, 2005; Haxby et al., 2000; Ishai, 2008; Pitcher, Walsh, & Duchaine, 2011).

Of the two extrastriate face-selective regions, the FFA has been studied more extensively. It shows a greater BOLD response to human faces than to inanimate objects, animals, and other human body parts (Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher et al., 1997; Kanwisher, Stanley, & Harris, 1999). Furthermore, lesions of this region in the right fusiform gyrus impair discrimination of the spatial configuration of facial features in acquired prosopagnosics (Barton, Press, Keenan, & O'Connor, 2002). Several studies have found that

the FFA plays a role not only in face detection, but also in the discrimination of face identity (Andrews & Ewbank, 2004; Gauthier et al., 2000; Grill-Spector et al., 2004; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston et al., 2004). There is mixed evidence for whether the FFA may also be sensitive to facial expressions (Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Winston et al., 2004). A more recent study suggests that the crucial factor determining the involvement of the FFA is whether the task relies more upon configural than feature-based processing of faces (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010). Discrimination of facial identity relies predominantly on configural processing, whereas facial expression recognition may be accomplished through either a configural or a feature-based analysis (Calder, Young, Keane, & Dean, 2000; Mondloch, Geldart, Maurer, & Grand, 2003).

A substantial amount of research has focused on the way that emotions are recognized from facial expressions (Adolphs, 2002). One area that appears to be involved in processing facial expressions and other dynamic aspects of faces is the superior temporal sulcus (STS). Single-unit recordings from monkeys have found neurons in the STS selective for both facial expressions (Hasselmo, Rolls, & Baylis, 1989) and gaze direction (Perrett, Hietanen, Oram, Benson, & Rolls, 1992). A role for the human STS in the analysis of both facial expressions and gaze is also supported by neuroimaging studies (Engell & Haxby, 2007; Hoffman & Haxby, 2000; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001; Phillips et al., 1998).

Other brain regions are involved in perceiving specific emotions from facial expressions. Damage to the amygdala can result in an impaired ability to recognize negative emotional expressions, especially fear (Adolphs et al., 1999; Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Broks et al., 1998; Calder et al., 1996; Young et al., 1995; Young, Hellawell, Van de Wal, & Johnson, 1996). In healthy participants, the amygdala is activated in response to fearful facial expressions (Morris et al., 1996, 1998; Phillips et al., 1997, 1998; Whalen et al., 2001), even when they are presented subliminally (Whalen et al., 1998; Williams, Morris, McGlone, Abbott, &

Mattingley, 2004). Amygdala lesions are also associated with impaired fear conditioning (Bechara et al., 1995; LaBar, LeDoux, Spencer, & Phelps, 1995) and a reduced capacity for experiencing fear (Feinstein, Adolphs, Damasio, & Tranel, 2011; Sprengelmeyer et al., 1999), indicating that the amygdala is involved in both the subjective experience of fear and the recognition of fear in others.

Similarly, lesions of the insula have yielded deficits in both experiencing and recognizing disgust (Adolphs, Tranel, & Damasio, 2003; Calder, Keane, Manes, Antoun, & Young, 2000), and the insula responds preferentially to disgusted facial expressions in healthy human participants (Phillips et al., 1997, 1998; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998). Additionally, the orbitofrontal cortex has been implicated in facial expression processing, particularly when explicit emotion recognition is required (Hornak, Rolls, & Wade, 1996; Nakamura et al., 1999; Narumoto et al., 2001). Some studies suggest that the orbitofrontal cortex is especially involved in processing angry facial expressions (Blair, Morris, Frith, Perrett, & Dolan, 1999; Harmer, Thilo, Rothwell, & Goodwin, 2001), consistent with the idea that understanding angry expressions may require contextual information and knowledge of social contingencies (Pichon, de Gelder, & Grèzes, 2009).

One way in which facial expressions may be recognized is through somatosensory resonance, a process in which the facial expressions of others are simulated at a sub-phenomenal level within the observer's own somatosensory and motor systems (Adolphs, 2002; Damasio, 1994). An embodied facial expression simulation mechanism would aid emotion recognition by allowing a direct experience of the other's emotional state. The idea that simulation facilitates emotion recognition is supported by the aforementioned lesion studies showing that damage to the amygdala and the insula impacts both the experience and the recognition of fear and disgust, respectively (Adolphs et al., 1999; Adolphs et al., 2003; Adolphs et al., 1994, 1995; Broks et al., 1998; Calder et al., 1996; Calder, Keane, et al., 2000; Feinstein

et al., 2011; Sprengelmeyer et al., 1999; Young et al., 1995, 1996). Patients with lesions in the somatosensory cortices of the right anterior parietal lobe also exhibit impaired recognition of emotion from facial expressions, especially fear (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Adolphs, Damasio, Tranel, & Damasio, 1996). Furthermore, disrupting the right primary somatosensory cortex with TMS specifically impairs recognition of fearful facial expressions (Pourtois et al., 2004). These findings indicate that simulating the sensorimotor components of expressing an emotion can also aid recognition of other's emotional expressions, particularly fearful expressions. What is more, seeing fearful human faces enhances detection of near-threshold tactile stimuli on the observer's own face, supporting the idea that activity in early somatosensory cortices is modulated by the sight of fearful facial expressions (Cardini, Bertini, et al., 2012).

From an evolutionary perspective, the emotional expressions of non-human animals also carry important information for the human observer. They may indicate whether the animal has aggressive or cooperative intentions, or signal the presence of potential rewards or threats, such as common food sources or predators. Despite being a source of valuable information for adaptive behavior, few studies have investigated heterospecific facial expression recognition (Bloom & Friedman, 2013; Kanazawa, 1996; Racca, Guo, Meints, & Mills, 2012) and none have examined whether non-human facial expressions are recognized via somatosensory simulation. As with human facial expressions, somatosensory simulation could benefit the observer by providing a direct understanding of the animal's emotional state. One way to investigate this question would be to test whether the sight of touch on emotional, non-human faces modulates tactile perception, which would suggest that non-human facial expressions are likewise processed in the somatosensory system of the human observer.

3.2. Visual remapping of touch

The interaction between visual face processing and tactile perception can be explored with the visual remapping of touch (VRT) paradigm, wherein viewing touch on a face improves detection of near-threshold tactile stimuli on the observer's own face (Serino et al., 2008). Electro-tactile stimulation is calibrated to be stronger on one cheek than the other so that extinction of the weaker stimulus occurs approximately half the time that bilateral touch is administered. This pattern that mimics the perceptual deficits of patients with damage to the right brain hemisphere who extinguish contralesional stimuli when an ipsilesional stimulus of comparable strength is presented at the same time (Bender, 1952). In healthy participants, the detection rate of bilateral tactile stimulation increases when seeing a face being touched on both cheeks compared to both a non-face object being touched bilaterally and to a face being merely approached by two fingers. Because participants are told that the visual stimuli are non-informative about the task and that they should base their responses solely on what they feel on their own cheeks, this demonstrates an involuntary effect of visual input on a purely tactile task. Note that the VRT effect differs from the VET effect examined in Chapter 1 in that the observer views the body part being touched rather than the just body part by itself. As demonstrated by Experiment 4, viewing a tactile event on the body may have different consequences for somatosensory perception than viewing the body alone.

VRT is stronger when one views one's own face being touched than when one views another person's face being touched (Serino et al., 2008). When another person's face is seen, VRT is enhanced if that person is perceived as similar to the observer in terms of both physical characteristics and social group membership (Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009). Furthermore, the degree to which VRT is affected by the other person's ethnicity is mediated by the observer's own implicit racial bias, and can be ameliorated by synchronous, interpersonal visuo-tactile stimulation designed to increase the

perceived physical similarity between one's own face and the other person's face (Fini et al., 2013). These findings indicate that VRT is not a purely automatic, bottom-up process. Instead, it is influenced by social factors and by higher-order representations of oneself and others.

VRT is thought to depend upon a crossmodal effect wherein the sight of touch modulates activity in the observer's somatosensory cortex, even in the absence of any actual tactile stimulation (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer, Heinze, & Rotte, 2005; Schaefer, Xu, Flor, & Cohen, 2009). Similar to VET, the remapping of seen touch onto the neural system for tactile processing is thought to occur via feedback from multisensory (i.e., visuo-tactile) brain regions to SI and/or SII, which enhances tactile sensitivity on the corresponding region of the body surface (Keysers et al., 2004; Ro, Wallace, Hagedorn, Farné, & Pienkos, 2004; Schaefer et al., 2005). Supporting this idea, a functional magnetic resonance imaging study identified a network of fronto-parietal areas involved in VRT that includes the polymodal ventral premotor cortex and the face area of SI/SII (Cardini, Costantini, et al., 2011).

Experiment 5: Remapping of observed touch on human and non-human faces with emotional expressions

To date, VRT studies have only compared human faces to non-face objects, so it is not known whether the effect would extend to non-human faces. Several studies have shown that the human brain processes heterospecific faces differently than conspecific faces after infancy (Dahl, Wallraven, Bühlhoff, & Logothetis, 2009; de Haan, Pascalis, & Johnson, 2002; Neiworth, Hassett, & Sylvester, 2007; Pascalis & Bachevalier, 1998; Pascalis, de Haan, & Nelson, 2002; Scott, Shannon, & Nelson, 2005, 2006). Specifically, human faces are analyzed more holistically (Dahl et al., 2009; Neiworth et al., 2007) and more efficiently at an early stage of face processing (de Haan et al., 2002; Scott et al., 2005). Because of these processing differences,

and because VRT strength is mediated by perceived similarity to the other (Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009), one might predict that any VRT for non-human faces would be weaker than for human faces. Nevertheless, VRT might be enhanced if the non-human face expressed fear, a critical emotion for adaptive behavior. Fear recognition is a particularly important function because the fearful expressions of others often signal the presence of an immediate threat in the environment. Efficient recognition of these expressions would allow the observer to quickly enact defensive behaviors to avoid potential harm. Moreover, the recognition of fearful faces seems especially dependent upon simulation within somatosensory cortex relative to the recognition of other emotions from faces (Adolphs et al., 2000, 1996; Pourtois et al., 2004). In keeping with this finding, VRT is enhanced by fearful human faces but not by happy or angry faces (Cardini, Bertini, et al., 2012). Because fear recognition is important for adaptive behavior and especially dependent upon an embodied somatosensory simulation mechanism, seeing a fearful monkey face being touched might heighten an otherwise weak interspecies VRT effect.

Experiment 5 examined whether VRT would occur for touch observed on monkey faces, and whether its strength would be similarly modulated by the monkeys' emotional facial expressions as it is by human facial expressions. Participants reported unilateral or bilateral touch on their own cheeks while they watched fearful, happy, and neutral human or monkey faces being touched or merely approached by fingers. Based on the study by Cardini and colleagues (2012), a stronger VRT effect was expected for fearful human faces than for neutral or happy human faces. Furthermore, it was predicted that VRT would be weak at best for neutral and happy monkey faces, but stronger for fearful monkey faces because of the value of fear recognition for survival and the stronger representation of fearful expressions in somatosensory cortex (Adolphs et al., 2000, 1996; Pourtois et al., 2004).

Method

Participants

Two separate groups of healthy adult females were recruited. One group ($n = 12$), ranging from 23 to 28 years old ($M = 25.17$ years, $SD = 1.64$), performed a version of the emotional VRT task with monkey faces. The other group ($n = 14$), ranging from 22 to 25 years old ($M = 23.05$ years, $SD = 0.60$), performed the standard emotional VRT task with human faces. All participants had normal or corrected-to-normal vision and reported a normal sense of touch. Participants gave written informed consent to participate and were treated in accordance with the ethical standards of the 1964 Declaration of Helsinki. The study was approved by of the Ethics Committee for Psychological Research at the Department of Psychology of the University of Bologna.

Materials

Four female human faces and four monkey faces showing fearful, happy, and neutral facial expressions were chosen. Human faces were taken from the Pictures of Facial Affect dataset (Ekman & Friesen, 1976). Monkey faces were gathered from the internet and selected based on emotion categorization and intensity ratings from a separate group of volunteers. (See the Pilot Data section under Results.) Short (3000 ms) videos were created in Microsoft PowerPoint that showed each face on a black background being either touched or approached by one or two human fingers. Care was taken with the monkey videos to ensure that the faces were touched in the less hairy region of skin below the eyes, in case remapping of the seen touch would be hindered by a difficulty in simulating the quality of touch to hairy monkey skin. A computer running C.I.R.O software (<http://www.cnc.unibo.psice.unibo/ciro>) displayed the visual stimuli and collected responses. Electro-tactile stimulation was delivered via two constant

current electrical stimulators (DS7A, Digitimer) connected to two pairs of electrodes (Neuroline, AMBU), one on each side of the participant's face over the zygomatic arch.

Procedure

Following the staircase procedure used by Cardini and colleagues (2012), the detection rate of electro-tactile stimulation was set to nearly 100% on one cheek and to approximately 60% on the other. The cheek that received stronger electro-tactile stimulation (left or right) was counterbalanced between participants. Confirming correct calibration, the mean detection rate of bilateral tactile stimulation across all experimental conditions was 51.74% ($SD = \pm 5.78\%$), and, when bilateral stimulation was not correctly identified, errors mostly consisted of reporting unilateral stimulation on the stronger side ($M = 95.40\%$ of errors, $SD = \pm 7.89\%$).

The experiment consisted of three blocks of VRT trials, one with neutral faces, one with fearful faces, and one with happy faces. Block order was counterbalanced between participants, and electro-tactile detection thresholds were re-calibrated between blocks. Each trial began with a face in the center of the screen and two fingers at the bottom of the screen on either side of the chin. One or both of the fingers then moved upward and either touched the cheek on the same side of the screen or touched a location about 5 cm lateral to the face before returning to the bottom of the screen. When the fingers reached the top of their trajectory (approximately 1000 ms into the trial), electro-tactile stimulation was delivered to one or both of the participant's cheeks (Figure 3.1). Participants used a keyboard to indicate whether they felt touch on the left cheek (the "D" key), on the right cheek (the "K" key), or on both cheeks (the space bar). They were instructed to respond as quickly and accurately as possible, and informed that the location of apparent touch on the cheeks of the other face was non-informative about the touch on their own face. Each trial combined one of two types of tactile stimulation (unilateral or bilateral), one of two types of visual stimulation (unilateral or bilateral), and one of

two types of finger trajectories (touch or no-touch), resulting in 8 trial types that were repeated 12 times in each block for a total of 96 trials per block, presented in a random order. Only trials with both bilateral tactile stimulation and bilateral finger movement (touch or no-touch) were analyzed.

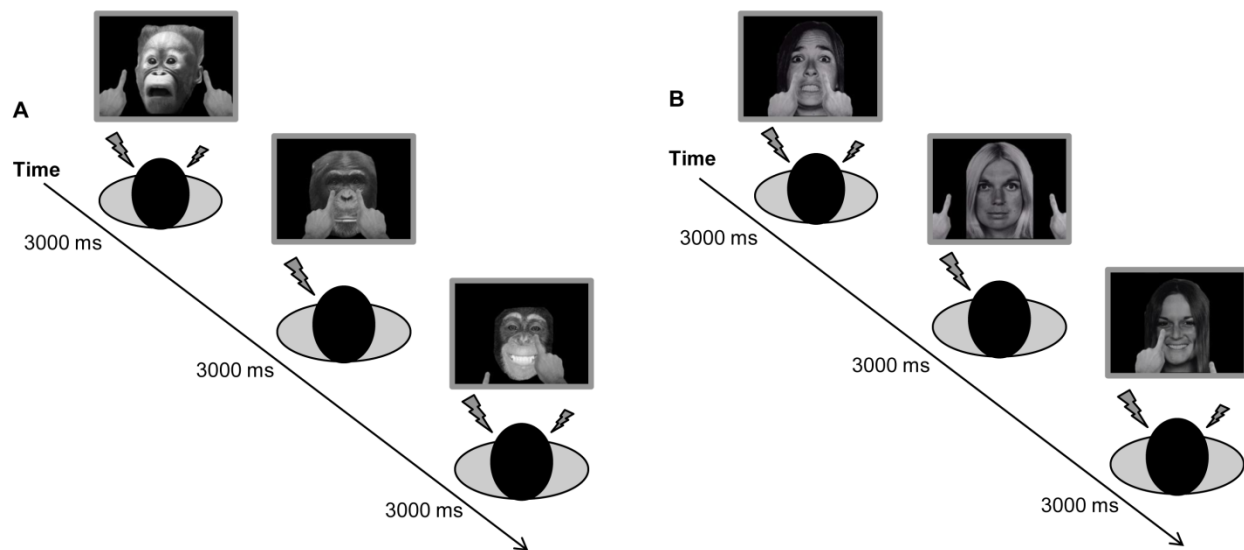


Figure 3.1. Sample trials from the group that saw monkey faces (A) and the group that saw human faces (B). Each trial combined one of two types of tactile stimulation (unilateral or bilateral), one of two types of visual stimulation (unilateral or bilateral), and one of two types of finger trajectory (touch or no-touch). Note that each block contained only one type of facial expression. Fearful, neutral, and happy expressions are shown together in this figure for illustrative purposes only.

Results

Pilot Data

A group of 32 volunteers categorized 26 monkey facial expressions as either happy, sad, angry, fearful, or neutral, and rated the intensity of each emotional expression on a scale

from 1 (“not at all intense”) to 6 (“very intense”). Emotion categorization and intensity data for the 12 monkey expressions selected for the main experiment are shown in Table 3.1. To analyze the emotion categorization data, scores of 1 and 0 were assigned to instances of correct and incorrect categorization, respectively, and the mean score for each participant in each expression category (fearful, happy, and neutral) was calculated. These mean scores were then entered into a Friedman’s ANOVA for non-parametric data, which showed a significant difference between accuracy of emotion categorization in the three categories, $\chi^2(2) = 34.81, p < .001$. Post-hoc Wilcoxon signed-rank tests showed that neutral facial expressions were correctly categorized less often than fearful ($p < .001$) or happy ($p < .001$) expressions, which did not differ from each other in emotion categorization accuracy ($p = .750$). Because participants were engaged in an emotion categorization task, they may have looked for subtle emotional signals in neutral faces that they would not otherwise have attended to. Importantly, neutral faces were still identified as neutral 71.88% of the time, and they were not consistently miscategorized as a certain emotion. Among the instances of neutral face miscategorizations, 52.78% were sadness misidentifications, 33.33% were happiness misidentifications, and 13.89% were anger misidentifications.

Table 3.1. Emotion categorization and intensity ratings for monkey facial expressions.

Facial Expression	Face Identity	Categorization Accuracy	Mean Intensity Rating
Fear	Face 1	100.00%	5.03
	Face 2	100.00%	4.44
	Face 3	96.88%	4.91
	Face 4	96.88%	5.25
	Mean	98.44%	4.91
Happiness	Face 1	100.00%	4.84
	Face 2	93.75%	4.66
	Face 3	96.88%	4.34
	Face 4	96.88%	4.38
	Mean	96.88%	4.55
Neutral	Face 1	75.00%	3.21
	Face 2	75.00%	3.73
	Face 3	65.63%	3.17
	Face 4	71.88%	4.14
	Mean	71.88%	3.56

Note. Participants in the pilot study categorized each facial expression as happy, sad, angry, fearful, or neutral, and then rated the intensity of each expression on a scale from 1 (“not at all intense”) to 6 (“very intense”).

Shapiro-Wilk tests indicated that intensity ratings were not normally distributed, so they were also analyzed with a Friedman’s ANOVA. Intensity ratings differed significantly among the facial expression categories, $\chi^2(2) = 38.58, p < .001$. Wilcoxon signed-rank tests revealed that neutral expressions were perceived to be less intense than fearful ($p < .001$) and happy ($p < .001$) expressions, and happy expressions were also perceived to be less intense than fearful expressions ($p = .010$). It is appropriate that the neutral faces should be perceived to be less intense than either type of emotional expression. Though the fearful and happy faces were not equivalent in terms of emotion intensity, this would only impede interpretation of the results if a stronger VRT effect were to be found for touch observed on fearful monkey faces than on happy monkey faces. On the contrary, although both fearful and happy monkey faces were perceived

to be quite intense, neither resulted in VRT. (See the next section for detailed results of the main experiment.)

Main Experiment

An analysis of variance (ANOVA) with the between-subjects factor of species (human or monkey) and within-subjects factors of facial expression (fearful, happy, or neutral) and finger trajectory (touch or no-touch) was conducted on the proportions of correct bilateral responses in each condition. None of the main effects were significant, but there was a two-way interaction between finger trajectory and species, $F(1, 24) = 9.01, p = .006$, partial $\eta^2 = .273$, and a three-way interaction between facial expression, finger trajectory, and species, $F(2, 48) = 3.21, p = .049$, partial $\eta^2 = .118$. To elucidate these interactions, two separate 3 (facial expression) x 2 (finger trajectory) within-subjects ANOVAs were conducted, one on the data from the group that saw monkey faces and another on the data from the group that saw human faces. There were no main effects from the monkey face group, nor was the interaction significant ($p \geq .277$ in all cases), indicating that VRT did not occur in any of the monkey expression conditions (Figure 3.2). In the human face group, there was a main effect of finger trajectory, $F(1, 13) = 30.72, p < .001$, partial $\eta^2 = .703$, with higher accuracy in bilateral touch trials ($M = 70.20\%$, $SEM = \pm 2.71\%$) than in bilateral no-touch trials ($M = 58.28\%$, $SEM = \pm 3.05\%$). There was also an interaction between facial expression and finger trajectory, $F(2, 26) = 9.94, p = .001$, partial $\eta^2 = .433$. T-tests comparing the VRT effect (the bilateral detection rate in the touch condition minus the bilateral detection rate in the no-touch condition) in the three human expression conditions (Fear Touch – No-Touch: $M = 20.48\%$, $SEM = \pm 3.68\%$; Happy Touch – No-Touch: $M = 4.33\%$, $SEM = \pm 2.34\%$; Neutral Touch – No-Touch: $M = 10.96\%$, $SEM = \pm 2.85\%$) showed that VRT was greater for fearful faces than for happy faces, $t(13) = 4.13, p = .001$, and neutral faces, $t(13) = 2.57, p = .023$ (Figure 3.2). The VRT effect for neutral faces also seemed to be greater than for happy faces, though this difference did not reach significance, $t(13) = -2.02, p = .064$.

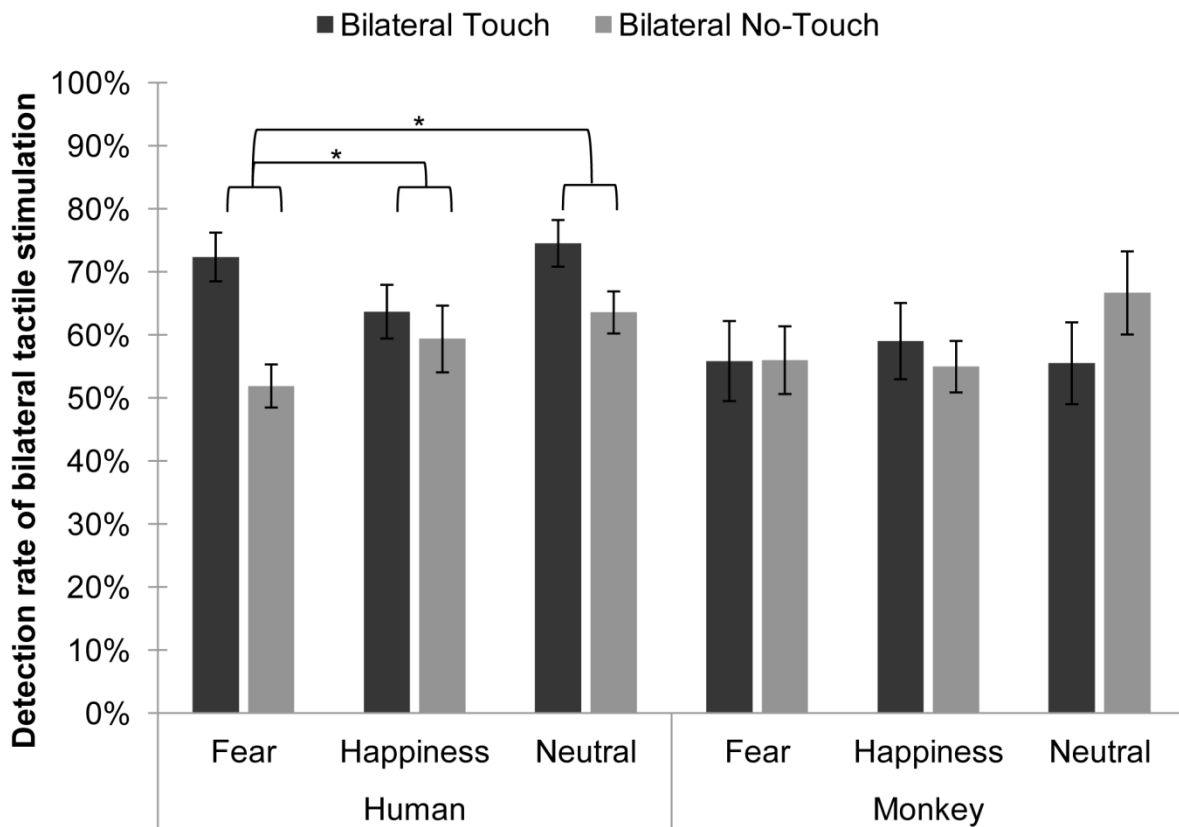


Figure 3.2. Mean (\pm SEM) detection rates of bilateral tactile stimulation in each condition. Asterisks indicate significant ($p < .050$) differences in the magnitude of VRT (bilateral detection rate in the touch condition minus bilateral detection rate in the no-touch condition) between facial expression conditions in the group that saw human faces. No such comparisons were made in the group that saw monkey faces because the 3 (facial expression) \times 2 (finger trajectory) ANOVA was not significant.

Discussion

Corroborating previous studies, seeing a human face being touched improved detection of near-threshold tactile stimuli simultaneously delivered to the observer's own face (Cardini, Costantini, et al., 2011; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009; Serino et al., 2008), and this effect was enhanced by fearful facial expressions compared to neutral or happy ones (Cardini, Bertini, et al., 2012). This is consistent with fear recognition being particularly dependent upon embodied simulation in somatosensory cortex (Adolphs et al., 2000, 1996; Pourtois et al., 2004). A simulation mechanism of emotion recognition might be especially valuable for recognizing emotions such as fear that indicate an immediate threat to survival, as the direct experience of the emotion might allow an observer to quickly identify and react to the threat.

Because the human brain processes human and non-human faces differently (Dahl et al., 2009; de Haan et al., 2002; Neiworth et al., 2007; Pascalis & Bachevalier, 1998; Pascalis et al., 2002; Scott et al., 2005, 2006) and the VRT effect is mediated by perceived similarity to the other (Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009), it was expected that any VRT effect for monkey faces overall would be minimal. This hypothesis was borne out. While the standard increase in bilateral tactile perception for touch trials was observed with human faces, the group that saw monkey faces did not exhibit this enhancement, suggesting that only observed touch on the faces of conspecifics is remapped onto the observer's own somatosensory cortex at a level capable of enhancing tactile perception on the face. Though some previous studies have found that even the sight of touch on inanimate objects triggers SII activity (Ebisch et al., 2008; Keysers et al., 2004), seeing touch on human body parts also modulates SI activity (Blakemore et al., 2005; Schaefer et al., 2005, 2009) and enhances SII activation beyond that found when viewing non-body objects being touched (Blakemore et al., 2005). Either or both of these differences might account for VRT

being specific to viewing touch on a body part (Serino et al., 2008). Experiment 5 further suggests that the remapping of seen touch onto somatosensory cortex in a manner that enhances tactile perception is not only specific to seeing touch on a body, but to seeing touch on a *human* body.

Contrary to expectations, showing monkey faces with fearful expressions did not increase tactile perception on touch trials compared to no-touch trials. Perhaps fearful monkey faces do not enhance VRT because there is no initial VRT effect for monkey faces to modulate, and the presence of a fearful expression in itself is not enough to influence tactile perception on the face. It is also possible that the fearful expressions of monkeys, unlike those of humans, are not processed via simulation in the observer's somatosensory system. To the authors' knowledge, no studies have directly investigated whether viewing monkey facial expressions modulates activity in human somatosensory cortex. Viewing non-emotional monkey face actions (biting and lip smacking) activates human mirror neuron systems in the inferior parietal lobule and the inferior frontal gyrus, which respond to both the execution and observation of actions (Buccino et al., 2004). Nevertheless, viewing fearful monkey faces, unlike fearful human faces, does not enhance amygdala activity compared to neutral (chewing) faces (Zhu et al., 2013). As the amygdala is involved in both expressing fear (Feinstein et al., 2011; Sprengelmeyer et al., 1999) and recognizing fear in others (Adolphs et al., 1999; Adolphs et al., 1994, 1995; Broks et al., 1998; Calder et al., 1996; Morris et al., 1996, 1998; Phillips et al., 1997, 1998; Whalen et al., 1998, 2001; Williams et al., 2004; Young et al., 1995, 1996), this could be taken as evidence that monkey facial expressions are not simulated in the same way as human facial expressions. Future studies should investigate whether recognizing the emotional facial expressions of non-human primates involves processing in somatosensory cortex, as does recognition of human facial expressions (Adolphs et al., 2000, 1996; Pourtois et al., 2004).

Note that, for the present study, the important factor was not the significance of the monkey's emotional expression to other monkeys but to the human participants. The monkey faces in the fearful and happy conditions were selected because they were consistently identified as fearful expressions or happy expressions in the pilot study (Table 3.1), which, like the main experiment, used volunteers who were novices in reading the emotional expressions of non-human primates. An interesting follow-up to this study would be to test people who work with monkeys and would therefore have more experience with identifying their emotional expressions. There is evidence that expertise with a species can improve recognition of their emotional expressions (Wan, Bolger, & Champagne, 2012) and change the way that their social body signals are processed in the brain (Kujala, Kujala, Carlson, & Hari, 2012). Future studies could examine whether such expertise could result in embodied simulation of the emotional expressions of non-human animals. Specifically, one could investigate whether experts in the social signals of a non-human species (e.g., animal trainers) remap observed touch on those animals onto their own somatosensory systems, and whether this potential VRT effect is modulated by the animal's emotional expression. In the case that experts do show a VRT effect for touch on the non-human animals they are familiar with, this would indicate that VRT is not restricted to conspecifics per se but to members of species with which one has interacted extensively, learning their non-verbal social cues. Furthermore, if this potential VRT effect were mediated by the emotional content of the facial or bodily expression, this would suggest that the embodied simulation mechanism of emotion recognition is also experience-dependent rather than strictly limited to conspecifics.

Conclusion

Seeing a human face being touched enhances detection of concurrent near-threshold tactile stimulation on the observer's own face (Cardini, Costantini, et al., 2011; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009; Serino et al.,

2008), and this visual remapping of touch (VRT) is heightened if the observed face expresses fear (Cardini, Bertini, et al., 2012). The present study demonstrated that VRT only occurs when seeing touch on human faces. Seeing a monkey's face being touched did not improve tactile perception compared to seeing the same face being merely approached by fingers, indicating that observed touch on non-human faces is not simulated within the human observer's somatosensory system. Furthermore, seeing a monkey face with a fearful expression being touched did not induce VRT, suggesting either that human observers do not simulate the emotional expressions of non-human animals in their own somatosensory systems or that the simulation of a fearful expression in itself is not enough to modulate tactile perception on the face.

The next chapter will investigate whether human facial expressions are equally important for another paradigm involving interpersonal visuo-tactile stimulation, the enfacement illusion (Bufalari et al., 2014; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Mazzurega et al., 2011; Paladino et al., 2010; Sforza et al., 2010; Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-Jiménez, Longo, et al., 2012; Tajadura-Jiménez et al., 2013; Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). Rather than measuring the effect of viewing a face being touched on tactile perception, enfacement measures the effect of an interpersonal multisensory experience on visual self-recognition and the perceived boundary between self and other.

Chapter 4: The enfacement illusion and the mental representation of one's own face

4.1. Visual self-recognition

Visual self-recognition has been studied across animal species using the mirror mark test (Gallup, Jr., 1970, 1977; Inoue-Nakamura, 1997; Marino, Reiss, & Gallup, Jr., 1994; Plotnik, de Waal, & Reiss, 2006; Prior, Schwarz, & Güntürkün, 2008; Reiss & Marino, 2001; Suarez & Gallup, Jr., 1981). In this test, a colored mark is covertly applied to the face of the animal, and then the animal's behavior in front of a mirror is observed. If the animal sees the mark in the mirror and investigates the corresponding spot on their own face, they are considered to exhibit visual self-recognition. The great apes demonstrate mirror self-recognition (Gallup, Jr., 1970, 1977; Inoue-Nakamura, 1997; Suarez & Gallup, Jr., 1981), and some studies have also found evidence for it in non-primate species such as bottlenose dolphins (Marino et al., 1994; Reiss & Marino, 2001), Asian elephants (Plotnik et al., 2006), and magpies (Prior et al., 2008). Human toddlers begin to pass the mirror mark test between 15 and 24 months of age (Amsterdam, 1972; Anderson, 1984; Nielsen & Dissanayake, 2004; Nielsen, Suddendorf, & Slaughter, 2006). This coincides with the development of other behaviors such as synchronic imitation and pretend play that require meta-representational capacities and mental representations of the self and others (Nielsen & Dissanayake, 2004). The mirror mark test is often taken as a hallmark of self-awareness in general (Gallup, Jr., 1970; Keenan, Gallup, Jr., & Falk, 2003), although more conservative accounts consider it to measure awareness of one's physical appearance only (Suddendorf & Butler, 2013).

In human adults, visual self-recognition tasks have found that one's own face is more salient and processed more efficiently than the faces of both familiar and unfamiliar others (Keenan et al., 1999; Keyes & Brady, 2010; Sui & Han, 2007; Tong & Nakayama, 1999). In

addition, viewing one's own face relative to the faces of familiar or unfamiliar others modulates the amplitude of the face-specific, posterior N170 component, as well as later ERP components over fronto-central sites (Keyes, Brady, Reilly, & Foxe, 2010; Sui, Zhu, & Han, 2006), regardless of whether the self-face stimuli are relevant to the task being performed (Sui et al., 2006).

These findings indicate that one's own face holds a unique status among visual face stimuli, and that enhanced visual processing of the self-face occurs automatically, even when it is unattended.

Visual self-recognition may also be assessed by having participants make judgments about the amount of their own face in morphs with another person's face. Studies using this method have found that people see more of their own face in morphs with the faces of others perceived as attractive (Epley & Whitchurch, 2008) and trustworthy (Verosky & Todorov, 2010). These findings indicate that, in addition to physical features, the social and emotional dimensions of faces can influence visual self-recognition. Furthermore, they are consistent with prior literature pointing to a self-enhancement bias, meaning that one tends to overestimate the positive characteristics of stimuli associated with oneself, including one's own face (Greenwald & Banaji, 1995).

Self-recognition studies showing facilitated visual processing of (Keenan et al., 1999; Keyes & Brady, 2010; Keyes et al., 2010; Sui & Han, 2007; Sui et al., 2006; Tong & Nakayama, 1999), and an implicit enhancement bias for (Epley & Whitchurch, 2008; Verosky & Todorov, 2010), one's own face suggest that there may be a specialized process for self-face perception above and beyond the mechanism by which the faces of others are perceived. Imaging studies seeking the neural basis of visual self-recognition have identified a fronto-parietal network, particularly in the right hemisphere, that extends beyond the regions typically implicated in face perception generally (see Devue & Brédart, 2011 for a review). This network for visual self-recognition includes a spatial representation of the self in the inferior parietal lobule and higher-

order evaluations of the self versus others in anterior areas such as the inferior frontal gyrus, the anterior cingulate cortex, and the anterior insula.

4.2. The enfacement illusion

While the studies described above focused on self-recognition through vision, more recent accounts of self-recognition have attempted to explain how the mental self-representation, including the self-face, is constructed and updated over time via the convergence of multimodal inputs (Apps & Tsakiris, 2014). This line of research has revealed that multisensory information can update the self-face representation, and, under certain circumstances, may blur the distinction between self and other. Seeing another person's face touched in synchrony with touch on one's own face—a procedure called interpersonal multisensory stimulation (IMS)—results in an “enfacement” illusion (Bufalari et al., 2014; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Mazzurega et al., 2011; Paladino et al., 2010; Sforza et al., 2010; Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-Jiménez, Longo, et al., 2012; Tajadura-Jiménez et al., 2013; Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). Concurrent visual and tactile inputs update the mental representation of the self-face, causing the subjects to accept more of the other person's facial features as their own (Bufalari et al., 2014; Sforza et al., 2010; Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-Jiménez et al., 2013; Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). The enfacement illusion has also been replicated using other measures of self/other merging, including the distance the participant chooses between two circles representing “self” and “other” (a variant of the Inclusion of the Other in the Self scale; Schubert & Otten, 2002) and a questionnaire assessing the subjective experience of the enfacement illusion adapted from the rubber hand illusion questionnaire (Bufalari et al., 2014; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Mazzurega et al., 2011; Paladino et al., 2010; Sforza et al., 2010; Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-

Jiménez, Longo, et al., 2012; Tajadura-Jiménez et al., 2013; Tajadura-Jiménez & Tsakiris, 2014).

Being interpersonal by definition, enfacement might be influenced by social and emotional dimensions of the IMS experience. Supporting this idea, the strength of the enfacement illusion is positively correlated with the participant's empathic traits, specifically the tendencies to adopt another person's point of view and to share the emotions and feelings of others (Sforza et al., 2010). The enfacement illusion is also stronger if the person observed during IMS was kind to the participant in a previous interaction (Bufalari et al., 2014). Moreover, the enfacement illusion can influence feelings of affinity with another person. Synchronous IMS increases participants' ratings of the other person's attractiveness, biases participants' inferences about the other's personality towards their own personality traits, and makes participants more influenced by the other person's estimate in a quantity estimation task (Paladino et al., 2010). A recent study also demonstrated that viewing a person from a different ethnic background being touched in synchrony with touch on one's own face can improve somatosensory resonance with the outgroup member (Fini et al., 2013).

Investigations into social and emotional influences on visual self-face recognition and the enfacement illusion have largely focused on positive interpersonal dimensions (e.g., empathy, attractiveness, and trustworthiness). The effect of negative valence on the enfacement illusion has not been explored as thoroughly. Moreover, no published study to date has examined how varying the emotion expressed by another person during an interpersonal visuo-tactile experience might impact the degree of self/other merging. Emotional facial expressions convey an intention to communicate, and may thus motivate greater effort on the part of the observer to understand the affective state of the other person. Fear is particularly important as a communicative signal because it usually indicates the presence of an immediate threat. Efficient and accurate recognition of a fearful facial expression confers both a private advantage to the observer by warning her of a potential threat to herself and a social benefit by facilitating

an appropriate reaction to the distress of her companion. One might predict that enfacement would be especially susceptible to fearful facial expressions because they carry such valuable information for the adaptive behavior of the observer.

Perhaps because they are important for both personal safety and social interaction, seeing fearful faces yields greater resonance in somatosensory cortex compared to seeing other emotional expressions. As discussed in the previous chapter, lesions of the right somatosensory cortices impair recognition of emotional facial expressions, especially fearful expressions (Adolphs et al., 2000, 1996). Similarly, inducing temporary, virtual lesions of the right somatosensory cortex with TMS impedes recognition of fearful but not happy facial expressions (Pourtois et al., 2004). Moreover, Experiment 5 replicated the previous finding (Cardini, Bertini, et al., 2012) that seeing a fearful human face being touched improves detection of near-threshold tactile stimulation on the observer's own face compared to seeing faces with neutral expressions or with other emotional expressions being touched. This suggests that fearful faces enhance somatosensory activity more than other facial expressions, including similarly negative expressions like anger. Lastly, a recent study found that enfacement of another person's face facilitated subsequent recognition of fear expressed by the assimilated face, but had no effect on recognition of happy or disgusted faces (Maister, Tsiakkas, & Tsakiris, 2013). This finding alludes to a potential interaction between the enfacement illusion and fearful facial expressions, perhaps because of the somatosensory cortical representation of fearful expressions.

To summarize, an observer who sees a fearful face might be more motivated to understand the other's affective state because of the value of the information that person is communicating. Achieving this understanding would entail simulating the other's emotional state, thereby activating the somatosensory cortex. During synchronous IMS, the somatosensory activation evoked by a fearful face, in combination with the somatosensory resonance induced by seeing another's face touched in synchrony with one's own (Cardini,

Costantini, et al., 2011; Cardini, Bertini, et al., 2012; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009; Serino et al., 2008), might increase enfacement beyond that obtained with neutral or emotional expressions of other kinds, including anger. Though angry expressions are similarly social and negative in valence, additional contextual information and knowledge of social contingencies are required to determine an appropriate reaction (Pichon et al., 2009). Moreover, the representation of anger in somatosensory cortex does not seem to be as strong as that of fear; whereas fearful facial expressions enhance remapping of seen touch onto the observer's own somatosensory system, the same is not true for angry expressions (Cardini, Bertini, et al., 2012). Therefore, one might predict stronger enfacement of a fearful face than an angry or a neutral face.

Experiment 6: The enfacement illusion is not affected by negative facial expressions

Experiment 6 examined whether varying the emotional content of human faces would affect the strength of the enfacement effect in the same way in which it affects the strength of VRT. In each experimental session, participants saw a fearful, an angry, or a neutral face being touched with a cotton swab either synchronously or asynchronously with a cotton swab touching their own face. Before and after this period of IMS, the participants watched a video of the same person's face (with a neutral expression) gradually morphing into their own face, and stopped the morph video as soon as it began to look more like their own face than the other person's face. The emotional expression of the other person in the morph video was not varied because the hypothesis was based on a fear-specific enhancement of somatosensory resonance. Thus, the crucial time for presentation of the emotional expression was the period in which participants saw the other person being touched while feeling touch on their own face. The difference in the amount of the other person's face in the frame where the participant stopped the morph video before and after synchronous IMS was taken as a measure of

enfacement. The asynchronous IMS session controlled for any effects of exposure to uncorrelated visual and tactile stimulation, as well as any effect of mere familiarity with the other person's face. A questionnaire was also used to assess the subjective strength of the enfacement illusion. It was predicted that enfacement would be comparable for neutral and angry faces, whereas seeing a fearful face would strengthen the enfacement effect due to enhanced somatosensory resonance and greater motivation to understand the other's affective state.

Method

Participants

Fifty-four female volunteers between 19 and 32 years old were recruited from the University of Bologna and randomly assigned to one of three experimental groups, resulting in three groups of 18 participants each (Fear group: 22-29 years old, $M = 25.06$ years, $SD = \pm 1.83$ years; Anger group: 23-32 years old, $M = 25.06$ years, $SD = \pm 2.21$ years; Neutral group: 19-28 years old, $M = 23.50$ years, $SD = \pm 2.43$ years). Participants in the Neutral group were only slightly younger on average than participants in the Fear group, $t(34) = 2.17$, $p = .037$, and the Anger group, $t(34) = 2.01$, $p = .053$. Each group saw a different emotional expression (fearful, angry, or neutral) during IMS. All participants had normal or corrected-to normal vision, reported normal tactile perception, and were naïve to the purpose of the experiment. They gave written informed consent to participate in the study, which was approved by of the Ethics Committee for Psychological Research at the University of Bologna Department of Psychology. They were treated in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Materials

Prior to the testing session, a photograph of each participant's face with a neutral expression was taken with a digital camera. The photographs were converted to black-and-white, mirror-transposed, and overlaid with an oval template on a black background to remove hair and ears. Photographs of six adult female volunteers who did not participate in the

experiment were obtained and processed in the same manner (except for the mirror-transposition) for use as the other-faces. Participant and other-face photographs were matched in luminance. These photographs were then blended in Adobe Photoshop 4 to create dynamic morph videos that progressed from 100% other-face to 100% self-face. The morph videos were 100 s long and progressed at a rate of 1% change in face per second, resulting in a prolonged and subtle morph. Each participant's face was morphed with two of the other-faces. Note that both the faces of the participants and the other-faces had neutral expressions in the morph videos.

Additionally, a camcorder was used to record videos of the other-faces being stroked on the left cheek with a cotton swab. Each video was in full color and 120 s long with strokes occurring approximately every 2 s. While being touched, each volunteer maintained a facial expression (fearful, angry, or neutral) for approximately 10 s, and this segment was then looped to produce the full 120 s video (Figure 4.1). To make the neutral videos appear more natural, and to ensure that all three video types showed some kind of facial movement, the neutral videos were created from looped segments that included eye blinks, mild head movements, and mild facial muscle contractions.



Figure 4.1. Frames from the angry, fearful, and neutral videos shown during IMS. Each participant saw videos from only one of the three facial expression categories. The assignment of each video to either the synchronous or the asynchronous IMS session was counterbalanced between participants.

The videos used for IMS were rated in a pilot study by a separate group of 25 female volunteers recruited from the same university as the participants in the main experiment ($M = 24.64$ years old, $SD = \pm 9.59$ years). These volunteers did not differ in age from the participants in the main experiment, $t(77) = -0.08$, $p = .940$. Volunteers in the pilot study categorized the emotional expressions in the videos (from the options of fear, happiness, surprise, disgust, anger, sadness, or neutral) and rated emotion intensity (from 1, “not at all,” to 7, “very much”). They also rated the attractiveness of the faces in the neutral photographs (from 1, “not at all,” to 7, “very much”) and how much the person in each video resembled their corresponding photograph (from 1, “not at all,” to 7, “it’s the same face”).

Presentation 15.0 was used to display the morph videos and the IMS videos, and to collect participants' responses. Additionally, after each stimulation session, participants completed a 14-item questionnaire to assess the strength of the subjective enfacement illusion experience. Table 4.1 contains the full text of this questionnaire, translated from Italian into English. Participants rated each statement on a scale of -3 (strongly disagree) to +3 (strongly agree), with 0 representing "neither agree nor disagree."

Table 4.1. Text of questionnaire items used to assess participants' subjective experience of the enfacement illusion.

Item	Item Text (translated from Italian)
01	While the other person's face was touched I seemed to feel the touch on my own face.
02	It seemed that the touch I felt on my face was caused by the cotton swab touching the other person's face.
03	It seemed that the other person's face was mine.
04	It seemed that the other person's face was part of my body.
05	It seemed that the other person's face belonged to me.
06	I seemed to see my face reflected in a mirror rather than the other person's face.
07	It seemed that the shape of the other person's face began to resemble mine.
08	It seemed that the skin color of the other face began to resemble mine.
09	It seemed that the features of the other person's face began to resemble mine.
10	It seemed that the other person's face would move if I moved.
11	I felt like I could control the other person's face.
12	I felt like I could not control my face.
13	I felt like I could not remember what my face looked like.
14	It seemed that sensation on my face was less vivid than normal.

Procedure

Participants completed one synchronous and one asynchronous IMS session, separated by at least 1 hour. Each participant saw only one type of facial expression in the IMS videos, either neutral, fearful, or angry. The order in which participants completed the IMS conditions was counterbalanced between participants within each group, as was the assignment of each other-face to either the synchronous or asynchronous IMS condition. A diagram of an experimental session is shown in Figure 4.2. In each session, participants first saw a morph

video that changed from 100% other-face to 100% self-face. They were instructed to stop the video as soon as it began to look more like their own face than the other person's face by pressing the "M" key. After this response, they watched a 120-s video of the other person continuously expressing either fear, anger, or a neutral expression while being stroked on the left cheek with a cotton swab. Concurrently, the participant was stroked on the right cheek (for specular correspondence) with a cotton swab either in synchrony or 1-s asynchrony with the touch in the video. Participants were instructed to sit still, to watch the face for the duration of the IMS video, and to attend to both the seen and the felt touch. Immediately after the IMS period, participants saw the same morph video as before and responded to it according to the same instructions. Finally, participants completed the illusion questionnaire at the end of each session. Questionnaire items were presented in a random order.

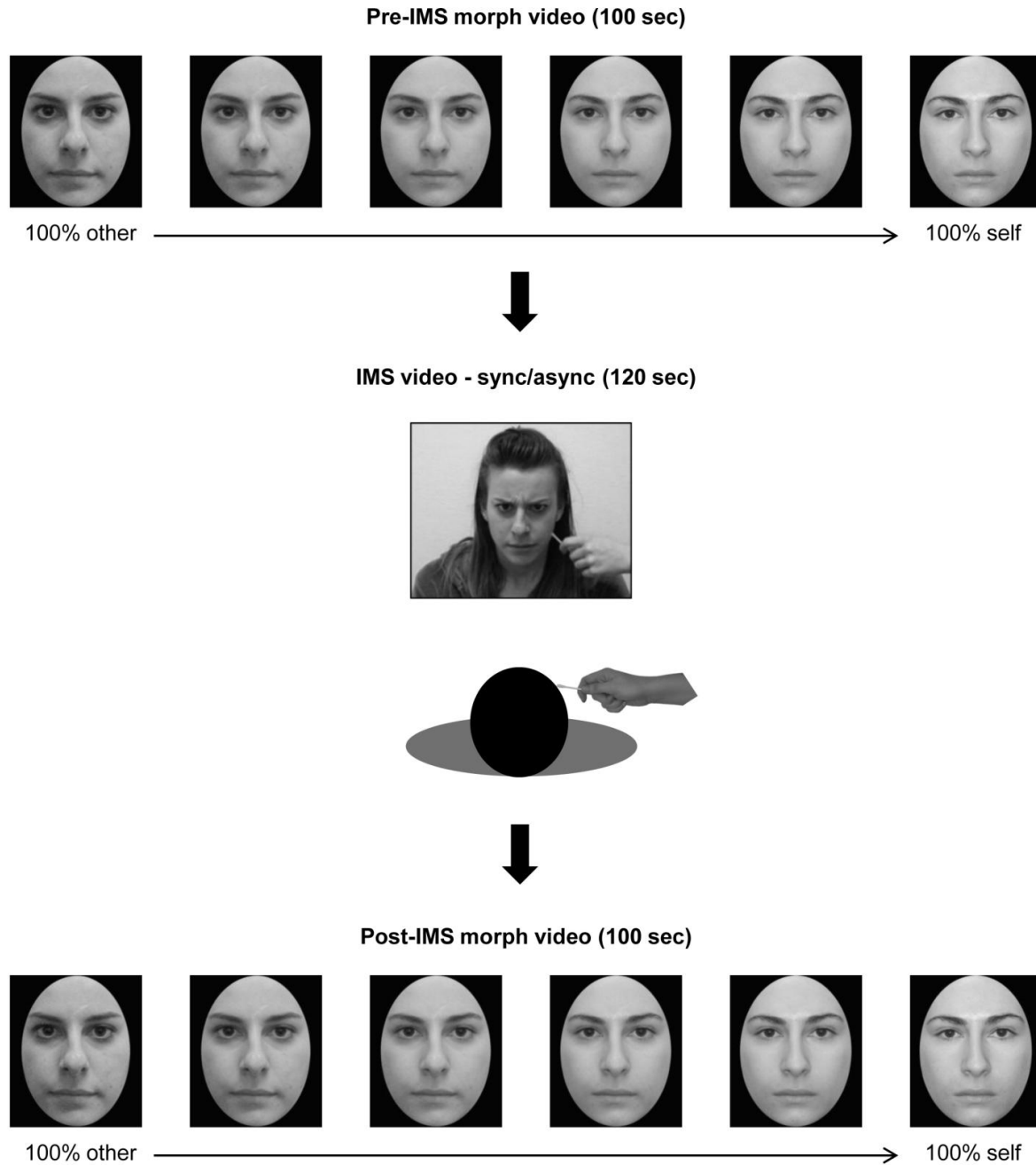


Figure 4.2. Diagram of an experimental session. Participants first watched an other-to-self morph video and pressed a button to stop it as soon as it began to look more like their face than the other person's face. This was followed by a period of synchronous or asynchronous IMS, and then a repetition of the morph video post-IMS. Morph videos were black-and-white, but IMS videos were shown in full color.

Design and Analysis

This experiment employed a 2 x 2 x 3 mixed factors design, with time (pre- or post-IMS) and IMS mode (synchronous or asynchronous) as within-subjects variables and facial expression (fearful, angry, or neutral) as a between-subjects variable. The key dependent variable was the amount of the other's face contained in the frame where participants stopped the morph video. Responses to the questionnaire items also served as a subjective measures of the enfacement illusion.

Results

Pilot Data

The pilot ratings of the IMS videos and the corresponding neutral face photographs of the same individuals used for the morph videos are shown in Table 4.2. Non-parametric tests were used for all analyses because the data were not normally distributed. A Cochran's Q test showed that recognition rates of the emotion expressed in each IMS video did not differ between the videos, $X^2(5) = 10.46, p = .067$.

Table 4.2. Pilot ratings of the IMS videos showing fearful, angry, and neutral expressions, and the corresponding photographs showing all the actors with neutral expressions.

Other-Face ^a	Emotion Recognition ^b	Emotion Intensity ^c	Photo Attractiveness ^c	Likeness to Photo ^c
Fear 1	92%	5.8	2.8	4.2
Fear 2	80%	5.5	3.7	3.8
Anger 1	76%	5.0	4.2	3.9
Anger 2	96%	5.6	2.8	6.0
Neutral 1	88%	5.7	4.2	4.3
Neutral 2	100%	5.9	3.1	5.0

^aEach row refers to the IMS video showing an emotional expression, as well as the corresponding neutral photograph of the same person used for the morph videos.

^bVolunteers chose between 7 emotion categories (fear, happiness, surprise, disgust, anger, sadness, or neutral).

°IMS video emotion intensity, photo attractiveness, and similarity of the face in the video to the face in the photo were rated on a scale of 1 (“not at all”) to 7 (“very much”).

Emotion intensity, attractiveness, and likeness-to-photograph ratings were analyzed with Friedman’s ANOVAs. Note that emotion intensity was rated from the IMS videos, whereas attractiveness ratings were based on the neutral photographs of the actors used in the morph videos. Likeness-to-photograph ratings were made by comparing the IMS video of each actor to her neutral photograph. The facial expressions in the six IMS videos were perceived as equally intense, $X^2(5) = 10.52$, $p = .062$. However, the photographs of the neutral faces differed in attractiveness, $X^2(5) = 37.91$, $p < .001$. Post-hoc Wilcoxon signed-rank tests with a Bonferroni correction for multiple comparisons showed that the neutral photographs corresponding to Neutral Video 1 and Anger Video 1 were perceived as more attractive than the neutral photographs corresponding to Neutral Video 2, Anger Video 2, and Fear Video 1 ($p < .003$, uncorrected, in all cases). To determine whether this might complicate interpretation of the data from the main experiment, another Friedman’s ANOVA was conducted on the average attractiveness ratings of the neutral photographs associated with each IMS video category. This test was not significant, $X^2(2) = 3.43$, $p = .184$, indicating that average attractiveness was well balanced across IMS emotion categories. It was not problematic that the neutral and anger conditions each contained one face that was perceived as more attractive than the other because the assignment of each other-face to the synchronous or the asynchronous IMS session was counterbalanced across participants.

The IMS videos also differed in likeness to their corresponding neutral photograph, $X^2(5) = 23.76$, $p < .001$. Wilcoxon signed-rank tests with a Bonferroni correction showed that Anger Video 2 was perceived as more similar to its corresponding neutral photograph than Fear Video 1, Fear Video 2, Neutral Video 1, and Anger Video 1 ($p < .003$ in all cases). The concern here would be that enfacement might be more easily detected when participants experience

synchronous IMS with Angry Video 2 because it is more obvious that the other-face in the morph video is the same as the face in the IMS video. To determine whether this was the case, a post-hoc independent samples t-test was performed on the change in when participants stopped the morph video before and after synchronous IMS for Anger Videos 1 and 2, because any difference in enfacement between these two conditions would not be due to a difference in the emotional expression. The amount of enfacement did not differ depending on which angry face participants saw being touched in synchrony with their own, $t(16) = 0.016$, $p = .987$. Thus, the higher likeness-to-photo rating given to Anger Video 1 did not bias the design by enhancing the ability of the morph video task to detect an enfacement effect when that stimulus was used.

Morph video analysis

A 2 x 2 x 3 mixed factors ANOVA with time (pre- or post-IMS) and IMS mode (synchronous or asynchronous) as within-subjects factors and the other's facial expression during IMS (fearful, angry, or neutral) as a between-subjects factor was conducted on the amount of the other person's face in the frame where participants stopped the morph video. This yielded a main effect of time, $F(1, 51) = 10.96$, $p = .002$, partial $\eta^2 = .177$, showing that, overall, participants stopped the morph videos sooner (at a frame containing less of their own face and more of the other person's face) after IMS than before.

More importantly, there was an interaction between time and IMS mode, $F(1, 51) = 8.96$, $p = .004$, partial $\eta^2 = .149$. Participants stopped the morph video at a frame containing more of the other person's face after synchronous IMS ($M = 52.57\%$, $SEM = \pm 1.75\%$) than they did before synchronous IMS ($M = 47.42\%$, $SEM = \pm 1.51\%$), $t(53) = -4.92$, $p < .001$, indicating that the experience of concurrent visual and tactile stimulation led them to accept more features of the other's face as their own. Importantly, in sessions with asynchronous IMS, there was no difference in the amount of the other person's face in the frame where participants stopped the morph video before ($M = 49.11\%$, $SEM = \pm 1.71\%$) and after ($M = 49.87\%$, $SEM = \pm 1.65\%$) IMS, $t(53) = -0.61$, $p = .542$, ruling out the possibility that mere exposure to the other's face with

temporally incongruent visual and tactile inputs could produce the same effect. These results are consistent with previous enfacement studies (Bufalari et al., 2014; Sforza et al., 2010; Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-Jiménez et al., 2013; Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). Pre-IMS morph video stopping points did not differ between synchronous and asynchronous IMS sessions, $t(53) = -0.91, p = .368$. The difference between post-IMS morph video stopping points in the synchronous and asynchronous IMS sessions was also non-significant, $t(53) = 1.55, p = .128$. Though one might expect enfacement to be reflected in a difference between the frame that participants chose after synchronous and asynchronous IMS, the crucial comparisons are between the post-IMS morph video judgment and the corresponding pre-IMS baseline judgment made in a single experimental session.

Surprisingly, the other person's facial expression during IMS had no impact on enfacement. There was no main effect of facial expression, $F(2, 51) = 2.84, p = .068$, partial $\eta^2 = .100$, no interaction between facial expression and time, $F(2, 51) = 0.38, p = .685$, partial $\eta^2 = .015$, or IMS mode, $F(2, 51) = 0.84, p = .439$, partial $\eta^2 = .032$, and, critically, no three-way interaction between emotion, time, and IMS, $F(2, 51) = 1.09, p = .344$, partial $\eta^2 = .041$. Contrary to the hypothesis, fearful faces did not increase enfacement relative to angry or neutral faces. In fact, the size of the enfacement effect was the same regardless of the emotion expressed by the other person during synchronous IMS (Figure 4.3).

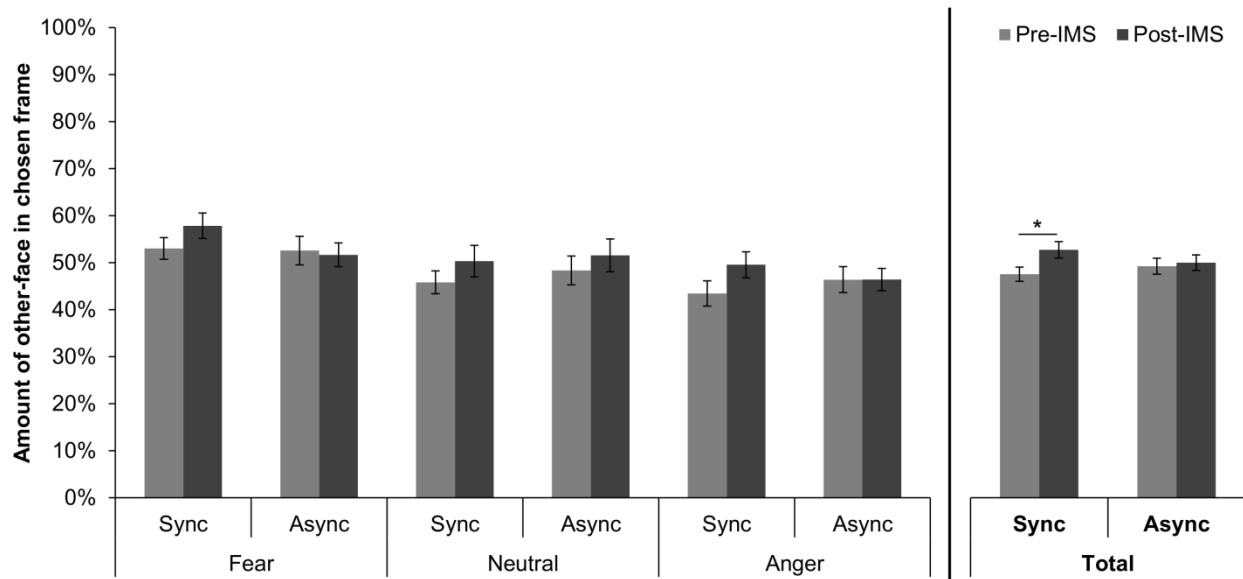


Figure 4.3. Mean percentage of other-face (\pm SEM) in the frame where participants stopped the morph video. Participants were instructed to stop the video as soon as the face began to look more like their own than the other person's. Enfacement is evident when participants stop the video at a frame containing more of the other person's face after synchronous IMS than before. * = $p < .050$.

To check whether differences in baseline, pre-IMS morph video judgments between groups might have obscured differences in the magnitude of enfacement between facial expression conditions, a 2 (IMS mode) x 3 (facial expression) mixed factors ANOVA was performed on the difference between the amount of the other person's face in the frame participants chose before and after IMS. This approach mitigates the baseline differences between groups. The analysis revealed a significant main effect of IMS mode, $F(1, 51) = 8.96$, $p = .004$, partial $\eta^2 = .149$, with a larger pre/post-IMS difference in the synchronous IMS session ($M = 5.15\%$, $SEM = \pm 1.05\%$) than in the asynchronous IMS session ($M = 0.76\%$, $SEM = \pm 1.24\%$). There was neither a main effect of facial expression, $F(2, 51) = 0.38$, $p = .685$, partial $\eta^2 = .015$, nor an interaction between IMS mode and facial expression, $F(2, 51) = 1.09$, $p = .344$,

partial $\eta^2 = .041$. These findings parallel the original analysis, indicating that any differences in baseline morph video judgments between groups did not obscure an effect of facial expression on the size of the enfacement illusion.

Questionnaire analysis

Shapiro-Wilk tests revealed that enfacement questionnaire responses were not normally distributed, so non-parametric tests were used for all analyses of the questionnaire data. Due to a computer error, questionnaire responses were not collected after the synchronous IMS session for one participant, so analyses are based on the responses of the remaining 53 participants. Two other participants failed to provide a valid response to one of the questionnaire items (Item 01 in the asynchronous session in one case, and Item 09 in the synchronous session in the other), so analyses of these questionnaire items are based on the data from the remaining 52 participants.

First, responses to each of the 14 questionnaire items were averaged across emotion conditions to look for a main effect of IMS mode (synchronous vs. asynchronous), with higher ratings of agreement predicted in the synchronous session than in the asynchronous session. Ratings were compared using a series of one-tailed Wilcoxon signed-rank tests with a Bonferroni correction to control the family-wise error rate. Participants gave higher ratings of agreement to 10 of the 14 illusion questionnaire items after synchronous relative to asynchronous IMS (Figure 4.4), indicating that synchronous IMS successfully induced a subjective illusion of self/other merging.

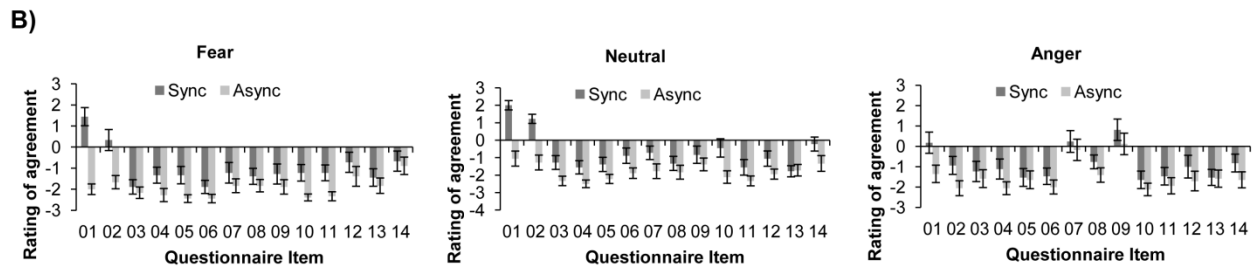
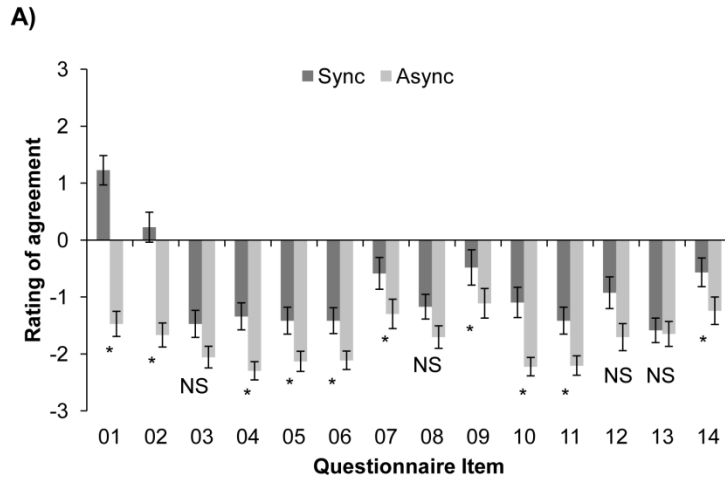


Figure 4.4. Mean (\pm SEM) ratings of agreement with enfacement illusion questionnaire items. Ratings were made on a Likert scale from -3 (strongly disagree) to 3 (strongly agree). Enfacement is evident in higher ratings of agreement after synchronous IMS than after asynchronous IMS. A) Mean ratings averaged across facial expression conditions. * = $p < .050$, one-tailed, after Bonferroni correction; NS = non-sig. B) Mean ratings in each facial expression condition. Note that there were no significant interactions between IMS mode and facial expression for any of the questionnaire items.

To test for an interaction between IMS mode and emotional expression, the differences between participants' ratings of each questionnaire item in the synchronous and asynchronous sessions were calculated (synchronous rating – asynchronous rating). These difference scores reflect the amount of enfacement that each participant experienced. Bonferroni-corrected Kruskal-Wallis tests were then used to look for differences in the strength of the enfacement

illusion between the groups that viewed fearful, angry, and neutral faces. No differences between emotion conditions were significant, again showing that enfacement was not influenced by the other person's facial expression.

Discussion

In the enfacement paradigm, synchronous interpersonal visual and tactile inputs update the self-face representation, causing the other person's face to be assimilated. It was hypothesized that seeing a fearful face being touched in synchrony with one's own face would increase enfacement because of greater motivation to understand the affective state of the other person, a process that would involve enhanced somatosensory resonance. It was also predicted that seeing an angry face being touched in synchrony with one's own face would *not* increase enfacement because anger is a more complex social emotion that requires additional contextual information to be properly understood (Pichon et al., 2009), and because angry expressions do not appear to be as strongly represented in the somatosensory system of the observer (Adolphs et al., 2000, 1996; Cardini, Bertini, et al., 2012). Contrary to the hypotheses, the strength of enfacement was the same regardless of the emotion expressed by the other person. Neither fearful nor angry facial expressions affected the amount of self/other merging produced by synchronous IMS.

Previous studies have shown that visual self-face recognition from self/other morphs is influenced by the affective valence of the other person's face, especially in terms of positive interpersonal dimensions such as attractiveness and trustworthiness (Epley & Whitchurch, 2008; Verosky & Todorov, 2010). In contrast, the present study did not find an effect of manipulating a social/emotional variable, namely the other person's facial expression, on self-face recognition from self/other morphs following the enfacement illusion. It is important to remember, however, that the morph videos always showed both the participant's face and the other person's face with *neutral* expressions. The emotion manipulation only occurred in the IMS video. The aim of the experiment was not to show a direct influence of the emotional

content of the self/other morph on self-face recognition, but to investigate whether seeing a fearful face would enhance somatosensory resonance, and thereby strengthen the enfacement illusion induced by synchronous IMS. Instead, varying the other person's facial expression did not influence the strength of enfacement. Moreover, these previous studies found an effect of positive interpersonal dimensions on self-face recognition from self/other morphs, whereas Experiment 6 investigated the effect of negative emotional expressions on the synchronous IMS procedure that induces enfacement.

Responses to the enfacement questionnaire further confirmed that participants experienced an illusion of enfacement, but this effect was not influenced by the other person's facial expression. Participants gave higher ratings of agreement to 10 of the 14 questionnaire items after synchronous IMS compared to asynchronous IMS, including statements assessing both self-identification (Items 01, 02, 04, 05, 06, 10, and 11) and physical similarity (Items 07, 09, and 14) (Tajadura-Jiménez, Longo, et al., 2012). Moreover, the differences between the ratings given to these questionnaire items in synchronous and asynchronous sessions did not change according to the emotion expressed during IMS. This suggests that the subjective experience of enfacement with emotional faces is both quantitatively and qualitatively similar to enfacement with neutral faces.

One might argue that visuo-motor congruence was not balanced across the three facial expression conditions in this experiment. The discrepancy between the facial movements of the actors in the fearful and angry videos and the participants' own facial muscles may have reduced the enfacement illusion, irrespective of any emotional component per se. However, it does not seem that visuo-motor incongruence was a major factor in the results. First, even the neutral videos included movements—eye blinks, mild head movements, and mild facial muscle contractions—that would have been incompatible with the participants' own. Thus, any effect of visuo-motor incongruence would have applied to all three facial expression conditions. In addition, a previous study on full-body illusions found that visuo-motor incongruence did not

affect the illusion induced by synchronous visuo-tactile stimulation (Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). Although that study investigated a different kind of illusion resulting from IMS, it suggests that visuo-motor congruence is relatively unimportant compared to visuo-tactile synchrony in these types of illusions.

Cardini and colleagues (2012) found that viewing fearful human faces being touched improves detection of near-threshold tactile stimuli on one's own face. This fear-specific enhancement of VRT was also replicated in Experiment 5. Experiment 6, on the other hand, did not find a fear-specific enhancement of enfacement. Although both the enfacement paradigm and the VRT paradigm involve presenting tactile stimuli on the participant's face while the participant views touch on another person's face, they actually measure quite different things. VRT measures the effect of congruent interpersonal visuo-tactile stimulation on a concurrent tactile detection task, which is directly related to activity in somatosensory cortex. Instead, enfacement measures *visual* self-face recognition *after* inducing an illusion with synchronous IMS. Modulation of somatosensory cortical activity by fearful facial expressions might not be expected to have as clear an effect on enfacement, which is essentially a self-recognition task, as it does in a tactile detection paradigm.

Maister and colleagues (2013) demonstrated that inducing an enfacement illusion enhances detection of fear when it is expressed by the person whose face was assimilated. As discussed earlier, somatosensory simulation seems to be particularly important for recognizing fearful facial expressions (Adolphs et al., 2000, 1996; Pourtois et al., 2004), so Maister and colleagues reasoned that synchronous IMS improved fear detection by enhancing resonance with somatosensory events on the other person's face. Nevertheless, the results of the present study suggest that this effect is not reciprocal. Viewing fearful facial expressions did not strengthen assimilation of the other person's face via synchronous IMS. This suggests that there is an asymmetric relationship between the multisensory interactions underlying enfacement and the processing of facial expressions.

A long-standing view of face perception holds that facial identity and facial expressions are processed independently (Bruce & Young, 1986; Haxby et al., 2000), allowing one to recognize individuals from their faces regardless of changes in expression. This view is supported by case studies of patients with impaired facial identity recognition but spared facial expression recognition (Duchaine et al., 2003; Humphreys et al., 2007; Sergent & Villemure, 1989; Tranel et al., 1988), as well as evidence for segregated processing of facial identity and facial expressions in healthy participants (Bobes et al., 2000; Eimer & Holmes, 2002; Sergent et al., 1994; Winston et al., 2004). Though more recent reports have challenged the idea of completely independent processing streams for facial identity and expressions, they still tend to support some degree of independence between the two functions (see Calder & Young, 2005 for a review). In fact, several studies have shown that facial identity influences facial expression processing, but not vice versa (Ellamil et al., 2008; Fox & Barton, 2007; Fox et al., 2008; Schweinberger & Soukup, 1998; Spangler et al., 2010). One could see how this asymmetric relationship between facial identity and facial expression processing might be beneficial. The identity of a familiar person provides additional information relevant to interpreting emotional expressions, such as knowledge of the individual's personality and prior interactions with them. On the other hand, it could be detrimental to identity recognition if dynamic facial attributes such as emotional expressions were to affect facial identity processing. The results of Experiment 6, together with the results of Maister and colleagues (2013), support an asymmetric relationship between facial identity and facial expression processing, and extend it into the domain of dynamic self-face recognition processes. While assimilation of another person's face into the self-face representation can affect perception of that person's facial expressions (Maister et al., 2013), the expression displayed by another person's face does not affect how readily that face is assimilated.

The asymmetric relationship between facial identity and facial expression processing may also shed light on why fearful expressions did not affect enfacement, in spite of their

significance for adaptive behavior. Fearful expressions usually signal the presence of an immediate threat in the observer's environment. Recognizing and reacting appropriately to fearful faces would therefore be critical for personal survival. Though this might make fearful faces especially salient, it does not necessarily follow that they should impact the process of visual self-face recognition, or even facial identity processing in general. As mentioned earlier, facial identity recognition might be hindered if it were easily influenced by dynamic facial expressions.

Though the present study did not find an effect of fearful or angry facial expressions on enfacement, it does not rule out the possibility that other facial expressions might modulate the illusion. In contrast to the asymmetric interaction model of facial identity and facial expression processing, some studies have found that happy facial expressions can facilitate the identification of faces as familiar (Endo, Endo, Kirita, & Maruyama, 1992; Kottoor, 1989; Sansone & Tiberghien, 1994). However, another study found that happy facial expressions increased the familiarity ratings of both familiar and unfamiliar faces (Baudouin, Gilbert, Sansone, & Tiberghien, 2000). This suggests that happy facial expressions might just bias the perceiver towards a feeling of familiarity rather than enhancing facial identity recognition per se. A later study demonstrated that happy facial expressions can also facilitate explicit recognition (i.e., naming) of famous faces (Gallegos & Tranel, 2005). Though the authors of that study argued that an internet search yielded at least as many photographs of their famous personalities with neutral expressions as with happy expressions, it is difficult to rule out the possibility that the facilitatory effect they found could be due to greater exposure to the smiling expressions of those celebrities. Despite the methodological issues with these studies, a future study could try the enfacement paradigm with happy facial expressions to determine whether smiling faces might affect the dynamic processes underlying self-face identification in a way that fearful and angry faces do not.

Another potential limitation of Experiment 6 is that participants' empathic traits were not measured. A previous study found that people with higher levels of both cognitive and emotional components of empathy tend to be more susceptible to the enfacement illusion (Sforza et al., 2010). Empathy may also influence reactions to emotional stimuli. For instance, participants high in emotional empathy show more automatic mimicry of happy and angry facial expressions (Sonnyby–Borgström, 2002). Additionally, cognitive empathy tends to primarily influence reactions to positive emotional stimuli, whereas emotional empathy influences reactions to negative emotional stimuli (Davis, Hull, Young, & Warren, 1987). It is thus possible that more empathic individuals might show differential enfacement effects depending on the other's facial expression. Future studies could explore the relationship between participant empathy and emotional expression in determining the strength of enfacement.

Conclusion

The results of Experiment 6 suggest that negative emotional facial expressions do not modulate the extent to which another's face is assimilated into the self-face representation following synchronous interpersonal visuo-tactile stimulation. Together with the results from a previous study showing that enfacement can enhance fear recognition (Maister et al., 2013), the results of Experiment 6 support an asymmetric interaction between facial expression processing and dynamic, multisensory processes of self-face identification. Further research is needed to determine whether this asymmetric interaction holds for all facial expression processing or is specific to negative emotional expressions.

General Discussion

I. Viewing the body versus viewing touch on the body

A common thread running through Experiments 1 through 6 is the interplay between vision of the body and cutaneous sensations. Nevertheless, an important distinction should be made between viewing a body being touched while also being touched, and viewing the body while being touched, but without seeing the touch itself. Experiments 1, 2, and 3 took the latter approach. Viewing the body without seeing the tactile event increases spatial tactile acuity (Cardini, Haggard, et al., 2013; Cardini, Longo, et al., 2012, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard et al., 2007; Harris et al., 2007; Kennett et al., 2001; Konen & Haggard, 2014; Press et al., 2004; Serino et al., 2007; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002, 2004), and the work presented here also shows that it reduces the discriminability of noxious heat intensities. Thus, non-informative vision of the body can specifically affect perceptual sensitivity in both tactile and nociceptive domains.

Previous studies indicate that visual enhancement of spatial tactile acuity occurs because of feedback from multisensory posterior parietal areas that modulate receptive field sizes in SI (Cardini, Longo, et al., 2011; Fiorio & Haggard, 2005; Haggard et al., 2007; Konen & Haggard, 2014; Serino, Padiglioni, et al., 2009; Taylor-Clarke et al., 2002). The results of Experiment 1 show that the anterior intraparietal sulcus only provides this feedback in the case of the personal route, when one's own body is seen. The intermediary for the interpersonal route, when another person's body is seen, remains to be determined. One candidate area could be the left angular gyrus in the inferior parietal lobule. Lesions in this region specifically impair visuo-spatial knowledge about the bodies of others, while leaving knowledge of the spatial configuration of one's own body intact (Degos et al., 1997; Felician et al., 2003). Future studies could test whether TMS targeting the left angular gyrus specifically disrupts VET when

viewing another person's body but not when viewing one's own body, which would implicate it as the source of modulation in interpersonal VET.

Importantly, the same mechanism that underlies the personal route for visual enhancement of spatial tactile acuity may also account for the reduced capacity to discriminate noxious heat intensities when viewing one's own body (Haggard et al., 2013). Several studies have demonstrated an association between disorganization of SI somatotopic maps and chronic pain (Flor et al., 1995; Flor et al., 1997; Maihöfner et al., 2003; Tecchio et al., 2002; Wrigley et al., 2009). Furthermore, tactile discrimination training can alleviate some forms of chronic pain (Flor, Denke, Schaefer, & Grüsser, 2001; Moseley & Wiech, 2009; Moseley, Zalucki, & Wiech, 2008). These results suggest that increased spatial tactile acuity correlates with diminished pain sensation. Nevertheless, the finding that viewing the body reduced sensitivity to noxious stimulation intensities but increased perceived pain levels overall is not entirely consistent with the interpretation of a common mechanism behind these two effects, nor with previous studies that described an analgesic effect of viewing the body (Longo et al., 2009, 2012; Mancini, Bolognini, et al., 2012; Mancini et al., 2013, 2011). Another possibility is that viewing the body decreases nociceptive sensitivity through modulation of SII rather than SI. Indeed, some consider the opercular-insular cortex to be the primary sensory area for nociception (Garcia-Larrea, 2012; Garcia-Larrea & Peyron, 2013), and TMS targeting SII, but not SI, impedes discrimination of noxious stimulus intensities (Lockwood et al., 2013). Future studies should explore the neural mechanism underlying visual modulation of pain perception, and whether it is distinct from that which underlies personal VET.

In Experiments 4, 5, and 6, participants instead viewed both the body itself and a tactile event on the body. Viewing a body (one's own or another person's) being touched improves detection of near-threshold tactile stimuli (Cardini, Costantini, et al., 2011; Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009; Serino et al., 2008).

Note that this effect could not occur via the same mechanism as visual enhancement of spatial tactile acuity. Viewing the body alone actually impairs performance on non-spatial tactile detection tasks (Harris et al., 2007; Press et al., 2004). Furthermore, sharpening of tactile receptive field sizes would not be expected to improve tactile detection in the same way that it would improve discrimination of the spatial properties of a tactile stimulus. Instead, viewing the body being touched may enhance tactile detection by modulating the baseline level of activity in somatosensory cortex. This “pre-activation” of somatosensory cortex might allow detection of weaker tactile stimuli.

Although viewing a noxious event on the hand in Experiment 4 did not elicit a significant effect relative to viewing the same stimulus on a non-body object, there was a trend toward increased nociceptive sensitivity when the hand was seen being touched by the thermode probe compared to when the object was seen being touched. Unlike with VRT, it is unclear whether this effect would result from a simple somatosensory pre-activation. While a change in the baseline activity level of the somatosensory cortex might alter the perceived intensity of both low and high pain stimuli, it would not necessarily enhance the ability to discriminate between them. In any case, the effect of viewing the body on cutaneous sensations appears to be highly sensitive to context, depending not only on whether the tactile event is also seen, but also on whether the cutaneous sensation is innocuous or noxious.

II. Self and other in visual-somatosensory interactions

The results of Experiments 1 through 6 also reveal differences in sensitivity to the identity of the observed body among the visual-somatosensory interactions investigated. On the surface, visual enhancement of spatial tactile acuity appeared to be insensitive to body identity because it occurred regardless of whether the observed body part belonged to oneself or to another person (Haggard, 2006). However, the findings of Experiment 1 revealed that

there are at least partially dissociable mechanisms behind VET when viewing one's own body and when viewing the body of another person. Therefore, VET is in fact sensitive to body identity, despite both the personal and interpersonal routes having similar consequences for tactile acuity. Although Experiments 2, 3, and 4 did not investigate the effect of viewing another person's body on perception of noxious stimuli, a previous study did not find any visual modulation of pain perception when participants saw the experimenter's hand rather than their own (Longo et al., 2009). This suggests that visual modulation of pain only operates via a personal route—that is, a functional network representing one's own body in particular rather than human bodies in general. This network might be akin to the dynamically updated multimodal representation of one's own body proposed by Sirigu and colleagues (1991) and by Schwoebel and Coslett (2005), including self-specific sensory inputs such as proprioception. A future study could test whether the human ventral intraparietal area is the source of pain modulation when viewing one's own body, as it is with visual modulation of spatial tactile acuity.

Previous studies had already demonstrated that visual remapping of touch is strongest when observing one's own face being touched (Cardini, Costantini, et al., 2011; Serino et al., 2008). When another person's face is seen being touched instead, VRT is strengthened when the other person is perceived as similar to oneself, but is still present to some extent even for dissimilar others such as outgroup members (Cardini, Tajadura-Jiménez, et al., 2013; Fini et al., 2013; Serino, Giovagnoli, et al., 2009). Beyond this, the constraints of face identity on the remapping process had not been explored. Experiment 5 revealed that seen touch is only remapped onto the human observer's own face when the other face is also human. This important limitation to VRT corroborates earlier evidence that non-human faces are processed differently than human faces (Dahl et al., 2009; de Haan et al., 2002; Neiworth et al., 2007; Pascalis & Bachevalier, 1998; Pascalis et al., 2002; Scott et al., 2005, 2006), and suggests that somatosensory resonance is strongest when viewing touch on another human.

III. Emotional modulations of visual-somatosensory interactions

Experiments 5 and 6 further elucidated the conditions under which emotional expressions will and will not influence interactions between vision and cutaneous sensations. Experiment 5 replicated a fear-specific enhancement of VRT relative to viewing happy or neutral facial expressions (Cardini, Bertini, et al., 2012). Moreover, this study also demonstrated that emotional facial expressions have no effect on the strength of VRT when non-human faces are observed being touched. These findings establish a limit to the emotional modulation of VRT, and suggest that the facial expressions of non-human animals may not be mapped onto the somatosensory system of the human observer in the same way that human facial expressions are. Whether this limitation is due to the degree of dissimilarity between the non-human face and the observer's own face or to a relative lack of expertise with non-human facial expressions remains to be determined.

In addition, Experiment 6 demonstrated that the enfacement illusion is not susceptible to facial expression manipulations, at least when negative expressions are used. Neither fearful nor angry expressions modulated the strength of enfacement relative to neutral expressions. This was initially surprising, as fearful expressions do enhance somatosensory resonance in the VRT paradigm (Cardini, Bertini, et al., 2012). Nevertheless, it seems that expressions of fear enhance remapping of observed touch on the other person's face, but do not influence feelings of ownership or identification with the other person. As discussed in Chapter 4, the findings of Experiment 6 also lend support to models positing an asymmetric interaction between processing of facial identity and facial expressions (Ellamil et al., 2008; Fox & Barton, 2007; Fox et al., 2008; Schweinberger & Soukup, 1998; Spangler et al., 2010). Although enfacement can improve fear recognition (Maister et al., 2013), fearful expressions do not strengthen the enfacement illusion.

IV. Concluding remarks

The experiments in this thesis have examined several interactions between vision and cutaneous sensations. Studying these interactions can shed light on the multiple levels of body representation in the brain. Vision and innocuous touch, for example, seem to interact within at least two levels of body representation: a visuo-spatial representation of human bodies in general, and a multimodal representation sensitive to proprioceptive cues and specific to one's own body (Schwoebel & Coslett, 2005; Sirigu et al., 1991). Moreover, even when vision of the body is non-informative about cutaneous sensation, it can specifically affect somatosensory discriminative capabilities. For example, viewing the body improves discrimination of the orientations of tactile gratings, an effect that, unlike an enhancement of tactile detection, could not result from a simple bias toward responding that a stimulus was present. In addition, viewing the body reduces the discriminability of noxious intensity levels, another effect that could not result from post-perceptual bias. These findings indicate that viewing the body does not merely prompt greater attention to sensations on the body, but actually affects sensory processing within the tactile and nociceptive systems.

Although viewing the body can have low-level sensory consequences for discrimination in the somatosensory domain, visuo-tactile interactions are also sensitive to higher-level processes such as the distinction between self and other (VET and VRT) and the perception of social and emotional cues (VRT). Lastly, while both self-recognition and emotion perception can influence visuo-tactile interactions, the enfacement illusion demonstrates that their relationship with each other is asymmetric. Together, these findings point to the existence of body representations in the brain that 1) link low-level perceptual analyses to processes underlying the perception of emotional cues and body/face identity, and 2) interact in complex ways depending upon contextual factors.

References

- Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews*, 1(1), 21–62. doi:10.1177/1534582302001001003
- Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, A. R. (2000). A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *The Journal of Neuroscience*, 20(7), 2683–2690.
- Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. (1996). Cortical systems for the recognition of emotion in facial expressions. *The Journal of Neuroscience*, 16(23), 7678–7687.
- Adolphs, R., Tranel, D., & Damasio, A. R. (2003). Dissociable neural systems for recognizing emotions. *Brain and Cognition*, 52(1), 61–69. doi:10.1016/S0278-2626(03)00009-5
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, 372(6507), 669–672. doi:10.1038/372669a0
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. R. (1995). Fear and the human amygdala. *The Journal of Neuroscience*, 15(9), 5879–5891.
- Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., ... Damasio, A. R. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia*, 37(10), 1111–1117. doi:10.1016/S0028-3932(99)00039-1
- Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental Psychobiology*, 5(4), 297–305. doi:10.1002/dev.420050403
- Anderson, J. R. (1984). The development of self-recognition: A review. *Developmental Psychobiology*, 17(1), 35–49. doi:10.1002/dev.420170104

- Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage*, *23*(3), 905–913. doi:10.1016/j.neuroimage.2004.07.060
- Apkarian, A. V., Bushnell, M. C., Treede, R.-D., & Zubieta, J.-K. (2005). Human brain mechanisms of pain perception and regulation in health and disease. *European Journal of Pain*, *9*(4), 463–463. doi:10.1016/j.ejpain.2004.11.001
- Apps, M. A. J., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. *Neuroscience & Biobehavioral Reviews*, *41*, 85–97. doi:10.1016/j.neubiorev.2013.01.029
- Armell, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1499–1506. doi:10.1098/rspb.2003.2364
- Arntz, A., Dreessen, L., & Merckelbach, H. (1991). Attention, not anxiety, influences pain. *Behaviour Research and Therapy*, *29*(1), 41–50. doi:10.1016/S0005-7967(09)80006-5
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, *7*(5), 542–548. doi:10.1038/nn1241
- Auclair, L., Noulhiane, M., Raibaut, P., & Amarenco, G. (2009). Where are your body parts? A pure case of heterotopagnosia following left parietal stroke. *Neurocase*, *15*(6), 459–465. doi:10.1080/13554790902911642
- 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. doi:10.1523/JNEUROSCI.2646-06.2007
- Banzett, R. B., Mulnier, H. E., Murphy, K., Rosen, S. D., Wise, R. J., & Adams, L. (2000). Breathlessness in humans activates insular cortex. *Neuroreport*, *11*(10), 2117–2120.

- Barton, J. J. S., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, *58*(1), 71–78. doi:10.1212/WNL.58.1.71
- Baudouin, J.-Y., Gilibert, D., Sansone, S., & Tiberghien, G. (2000). When the smile is a cue to familiarity. *Memory*, *8*(5), 285–292. doi:10.1080/09658210050117717
- Bechara, A., Tranel, D., Damasio, H., Adolphs, R., Rockland, C., & Damasio, A. R. (1995). Double dissociation of conditioning and declarative knowledge relative to the amygdala and hippocampus in humans. *Science*, *269*(5227), 1115–1118. doi:10.1126/science.7652558
- Bender, M. B. (1952). *Disorders in Perception: With Particular Reference to the Phenomena of Extinction and Displacement* (Vol. viii). Springfield, IL: Charles C. Thomas.
- Bessou, P., & Perl, E. R. (1969). Response of cutaneous sensory units with unmyelinated fibers to noxious stimuli. *Journal of Neurophysiology*, *32*(6), 1025–1043.
- Blair, R. J. R., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain*, *122*(5), 883–893. doi:10.1093/brain/122.5.883
- Blakemore, S.-J., Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. *Brain*, *128*(7), 1571–1583. doi:10.1093/brain/awh500
- Bloom, T., & Friedman, H. (2013). Classifying dogs' (*Canis familiaris*) facial expressions from photographs. *Behavioural Processes*, *96*, 1–10. doi:10.1016/j.beproc.2013.02.010
- Bobes, M. A., Martín, M., Olivares, E., & Valdés-Sosa, M. (2000). Different scalp topography of brain potentials related to expression and identity matching of faces. *Cognitive Brain Research*, *9*(3), 249–260. doi:10.1016/S0926-6410(00)00003-3
- Bornhövd, K., Quante, M., Glauche, V., Bromm, B., Weiller, C., & Büchel, C. (2002). Painful stimuli evoke different stimulus–response functions in the amygdala, prefrontal, insula

- and somatosensory cortex: A single-trial fMRI study. *Brain*, 125(6), 1326–1336.
doi:10.1093/brain/awf137
- Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature*, 391(6669), 756–756. doi:10.1038/35784
- Bremmer, F., Klam, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Visual–vestibular interactive responses in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, 16(8), 1569–1586. doi:10.1046/j.1460-9568.2002.02206.x
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., ... Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29(1), 287–296. doi:10.1016/S0896-6273(01)00198-2
- Broks, P., Young, A. W., Maratos, E. J., Coffey, P. J., Calder, A. J., Isaac, C. L., ... Hadley, D. (1998). Face processing impairments after encephalitis: Amygdala damage and recognition of fear. *Neuropsychologia*, 36(1), 59–70. doi:10.1016/S0028-3932(97)00105-X
- Brooks, J. C. W., Nurmikko, T. J., Bimson, W. E., Singh, K. D., & Roberts, N. (2002). fMRI of thermal pain: Effects of stimulus laterality and attention. *NeuroImage*, 15(2), 293–301. doi:10.1006/nimg.2001.0974
- Brooks, J. C. W., Zambreanu, L., Godinez, A., Craig, A. D., & Tracey, I. (2005). Somatotopic organisation of the human insula to painful heat studied with high resolution functional imaging. *NeuroImage*, 27(1), 201–209. doi:10.1016/j.neuroimage.2005.03.041
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, 77(3), 305–327. doi:10.1111/j.2044-8295.1986.tb02199.x
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., ... Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic

- manner: An fMRI study. *European Journal of Neuroscience*, 13(2), 400–404.
doi:10.1111/j.1460-9568.2001.01385.x
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., ... Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspicuous: An fMRI study. *Journal of Cognitive Neuroscience*, 16(1), 114–126.
doi:10.1162/089892904322755601
- Büchel, C., Bornhövd, K., Quante, M., Glauche, V., Bromm, B., & Weiller, C. (2002). Dissociable neural responses related to pain intensity, stimulus intensity, and stimulus awareness within the anterior cingulate cortex: A parametric single-trial laser functional magnetic resonance imaging study. *The Journal of Neuroscience*, 22(3), 970–976.
- Bufoalari, I., Lenggenhager, B., Porciello, G., Holmes, B. S., & Aglioti, S. M. (2014). Enfacing others but only if they are nice to you. *Frontiers in Behavioral Neuroscience*, 8.
doi:10.3389/fnbeh.2014.00102
- Burgess, P. R., & Perl, E. R. (1967). Myelinated afferent fibres responding specifically to noxious stimulation of the skin. *The Journal of Physiology*, 190(3), 541–562.
- Bushnell, M. C., Duncan, G. H., Dubner, R., Jones, R. L., & Maixner, W. (1985). Attentional influences on noxious and innocuous cutaneous heat detection in humans and monkeys. *Journal of Neuroscience*, 5(5), 1103–1110.
- Bushnell, M. C., Duncan, G. H., Hofbauer, R. K., Ha, B., Chen, J.-I., & Carrier, B. (1999). Pain perception: Is there a role for primary somatosensory cortex? *Proceedings of the National Academy of Sciences*, 96(14), 7705–7709. doi:10.1073/pnas.96.14.7705
- Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, 18(4), 289–306.
doi:10.1080/02643290126172

- Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience*, 3(11), 1077–1078. doi:10.1038/80586
- Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience*, 6(8), 641–651. doi:10.1038/nrn1724
- Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 527–551. doi:10.1037/0096-1523.26.2.527
- Calder, A. J., Young, A. W., Rowland, D., Perrett, D. I., Hodges, J. R., & Ectoff, N. L. (1996). Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear. *Cognitive Neuropsychology*, 13(5), 699–745. doi:10.1080/026432996381890
- Capelari, E. D. P., Uribe, C., & Brasil-Neto, J. P. (2009). Feeling pain in the rubber hand: Integration of visual, proprioceptive, and painful stimuli. *Perception*, 38(1), 92 – 99. doi:10.1068/p5892
- Cardinal, R. N., & Aitken, M. R. F. (2006). *ANOVA for the Behavioural Sciences Researcher*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Cardini, F., Bertini, C., Serino, A., & Làdavas, E. (2012). Emotional modulation of visual remapping of touch. *Emotion*, 12(5), 980–987. doi:10.1037/a0027351
- Cardini, F., Costantini, M., Galati, G., Romani, G. L., Làdavas, E., & Serino, A. (2011). Viewing one's own face being touched modulates tactile perception: An fMRI study. *Journal of Cognitive Neuroscience*, 23(3), 503–513. doi:10.1162/jocn.2010.21484
- Cardini, F., Haggard, P., & Làdavas, E. (2013). Seeing and feeling for self and other: Proprioceptive spatial location determines multisensory enhancement of touch. *Cognition*, 127(1), 84–92. doi:10.1016/j.cognition.2012.12.010

- Cardini, F., Longo, M. R., Driver, J., & Haggard, P. (2012). Rapid enhancement of touch from non-informative vision of the hand. *Neuropsychologia*, *50*(8), 1954–1960.
doi:10.1016/j.neuropsychologia.2012.04.020
- Cardini, F., Longo, M. R., & Haggard, P. (2011). Vision of the body modulates somatosensory intracortical inhibition. *Cerebral Cortex*, *21*(9), 2014–2022. doi:10.1093/cercor/bhq267
- Cardini, F., Tajadura-Jiménez, A., Serino, A., & Tsakiris, M. (2013). It feels like it's me: Interpersonal multisensory stimulation enhances visual remapping of touch from other to self. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(3), 630–637. doi:10.1037/a0031049
- Carlsson, K., Andersson, J., Petrovic, P., Petersson, K. M., Öhman, A., & Ingvar, M. (2006). Predictability modulates the affective and sensory-discriminative neural processing of pain. *NeuroImage*, *32*(4), 1804–1814. doi:10.1016/j.neuroimage.2006.05.027
- Cauda, F., Torta, D. M.-E., Sacco, K., Geda, E., D'Agata, F., Costa, T., ... Amanzio, M. (2012). Shared “core” areas between the pain and other task-related networks. *PLoS ONE*, *7*(8), e41929. doi:10.1371/journal.pone.0041929
- Chan, A. W.-Y., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *Neuroreport*, *15*(15), 2407–2410.
- Christensen, B. N., & Perl, E. R. (1970). Spinal neurons specifically excited by noxious or thermal stimuli: Marginal zone of the dorsal horn. *Journal of Neurophysiology*, *33*(2), 293–307.
- Cohen Kadosh, K., Henson, R. N. A., Cohen Kadosh, R., Johnson, M. H., & Dick, F. (2010). Task-dependent activation of face-sensitive cortex: An fMRI adaptation study. *Journal of Cognitive Neuroscience*, *22*(5), 903–917. doi:10.1162/jocn.2009.21224
- Colby, C. L., & Duhamel, J.-R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia*, *29*(6), 517–537.
doi:10.1016/0028-3932(91)90008-V

- Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, 16(2), 229–240.
doi:10.1016/j.concog.2007.01.001
- Costantini, M., Urgesi, C., Galati, G., Romani, G. L., & Aglioti, S. M. (2011). Haptic perception and body representation in lateral and medial occipito-temporal cortices. *Neuropsychologia*, 49(5), 821–829. doi:10.1016/j.neuropsychologia.2011.01.034
- Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience*, 3(8), 655–666. doi:10.1038/nrn894
- Craig, A. D. (2009). How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10(1), 59–70. doi:10.1038/nrn2555
- Craig, A. D., Chen, K., Bandy, D., & Reiman, E. M. (2000). Thermosensory activation of insular cortex. *Nature Neuroscience*, 3(2), 184–190. doi:10.1038/72131
- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7(2), 189–195.
doi:10.1038/nn1176
- Crombez, G., Baeyens, F., & Eelen, P. (1994). Sensory and temporal information about impending pain: The influence of predictability on pain. *Behaviour Research and Therapy*, 32(6), 611–622. doi:10.1016/0005-7967(94)90015-9
- Dahl, C. D., Wallraven, C., Bülthoff, H. H., & Logothetis, N. K. (2009). Humans and macaques employ similar face-processing strategies. *Current Biology*, 19(6), 509–513.
doi:10.1016/j.cub.2009.01.061
- Damasio, A. R. (1994). *Descartes' Error: Emotion, Reason, and the Human Brain*. New York: Putnam.
- Davidoff, R. A. (1990). The pyramidal tract. *Neurology*, 40(2), 332–339.

- Davis, M. H., Hull, J. G., Young, R. D., & Warren, G. G. (1987). Emotional reactions to dramatic film stimuli: The influence of cognitive and emotional empathy. *Journal of Personality and Social Psychology*, *52*(1), 126–133. doi:10.1037/0022-3514.52.1.126
- Decety, J., & Sommerville, J. A. (2003). Shared representations between self and other: A social cognitive neuroscience view. *Trends in Cognitive Sciences*, *7*(12), 527–533. doi:10.1016/j.tics.2003.10.004
- de Gelder, B., Van den Stock, J., Meeren, H. K. M., Sinke, C. B. A., Kret, M. E., & Tamietto, M. (2010). Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions. *Neuroscience & Biobehavioral Reviews*, *34*(4), 513–527. doi:10.1016/j.neubiorev.2009.10.008
- Degos, J. D., Bachoud-Levi, A. C., Ergis, A. M., Petrissans, J. L., & Cesaro, P. (1997). Selective inability to point to extrapersonal targets after left posterior parietal lesions: An objectivization disorder? *Neurocase*, *3*(1), 31–39. doi:10.1080/13554799708404032
- de Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. *Journal of Cognitive Neuroscience*, *14*(2), 199–209. doi:10.1162/089892902317236849
- Del Parigi, A., Gautier, J.-F., Chen, K., Salbe, A. D., Ravussin, E., Reiman, E., & Tataranni, P. A. (2002). Neuroimaging and obesity: Mapping the brain responses to hunger and satiation in humans using positron emission tomography. *Annals of the New York Academy of Sciences*, *967*, 389–397.
- Denes, G., Cappelletti, J. Y., Zilli, T., Dalla Porta, F., & Gallana, A. (2000). A category-specific deficit of spatial representation: The case of autotopagnosia. *Neuropsychologia*, *38*(4), 345–350. doi:10.1016/S0028-3932(99)00101-3
- De Renzi, E., & Scotti, G. (1970). Autotopagnosia: Fiction or reality? Report of a case. *Archives of Neurology*, *23*(3), 221–227. doi:10.1001/archneur.1970.00480270031005

- de Vignemont, F. (2014). Shared body representations and the “Whose” system. *Neuropsychologia*, *55*, 128–136. doi:10.1016/j.neuropsychologia.2013.08.013
- Devue, C., & Brédart, S. (2011). The neural correlates of visual self-recognition. *Consciousness and Cognition*, *20*(1), 40–51. doi:10.1016/j.concog.2010.09.007
- Dijkerman, H. C., & de Haan, E. H. F. (2007). Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences*, *30*(02), 189–201. doi:10.1017/S0140525X07001392
- Dong, W. K., Salonen, L. D., Kawakami, Y., Shiwaku, T., Kaukoranta, E. M., & Martin, R. F. (1989). Nociceptive responses of trigeminal neurons in SII-7b cortex of awake monkeys. *Brain Research*, *484*(1–2), 314–324. doi:10.1016/0006-8993(89)90375-2
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470–2473. doi:10.1126/science.1063414
- Duchaine, B. C., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception*, *32*(7), 827–838.
- 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.
- Dum, R. P., Levinthal, D. J., & Strick, P. L. (2009). The spinothalamic system targets motor and sensory areas in the cerebral cortex of monkeys. *The Journal of Neuroscience*, *29*(45), 14223–14235. doi:10.1523/JNEUROSCI.3398-09.2009
- Ebisch, S. J. H., Perrucci, M. G., Ferretti, A., Del Gratta, C., Romani, G. L., & Gallese, V. (2008). The sense of touch: Embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *Journal of Cognitive Neuroscience*, *20*(9), 1611–1623. doi:10.1162/jocn.2008.20111

- Egan, G., Silk, T., Zamarripa, F., Williams, J., Federico, P., Cunnington, R., ... Denton, D. (2003). Neural correlates of the emergence of consciousness of thirst. *Proceedings of the National Academy of Sciences*, *100*(25), 15241–15246.
doi:10.1073/pnas.2136650100
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, *317*(5841), 1048–1048. doi:10.1126/science.1142175
- 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*, *305*(5685), 875–877.
doi:10.1126/science.1097011
- Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences*, *104*(23), 9828–9833. doi:10.1073/pnas.0610011104
- Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, *13*(4), 427–431.
- Eisenberg, E., Chistyakov, A. V., Yudashkin, M., Kaplan, B., Hafner, H., & Feinsod, M. (2005). Evidence for cortical hyperexcitability of the affected limb representation area in CRPS: A psychophysical and transcranial magnetic stimulation study. *Pain*, *113*(1–2), 99–105.
doi:10.1016/j.pain.2004.09.030
- Ekman, P., & Friesen, W. V. (1976). *Pictures of Facial Affect*. Palo Alto, CA: Consulting Psychologists.
- Ellamil, M., Susskind, J. M., & Anderson, A. K. (2008). Examinations of identity invariance in facial expression adaptation. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(3), 273–281. doi:10.3758/CABN.8.3.273
- Endo, N., Endo, M., Kirita, T., & Maruyama, K. (1992). The effects of expression on face recognition. *Tohoku Psychologica Folia*, *51*, 37–44.

- Engell, A. D., & Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia*, *45*(14), 3234–3241.
doi:10.1016/j.neuropsychologia.2007.06.022
- Epley, N., & Whitchurch, E. (2008). Mirror, mirror on the wall: Enhancement in self-recognition. *Personality and Social Psychology Bulletin*, *34*(9), 1159–1170.
doi:10.1177/0146167208318601
- Farina, S., Tinazzi, M., Le Pera, D., & Valeriani, M. (2003). Pain-related modulation of the human motor cortex. *Neurological Research*, *25*(2), 130–142.
doi:10.1179/016164103101201283
- Farrell, M. J., Egan, G. F., Zamarripa, F., Shade, R., Blair-West, J., Fox, P., & Denton, D. A. (2006). Unique, common, and interacting cortical correlates of thirst and pain. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(7), 2416–2421. doi:10.1073/pnas.0511019103
- Feinstein, J. S., Adolphs, R., Damasio, A., & Tranel, D. (2011). The human amygdala and the induction and experience of fear. *Current Biology*, *21*(1), 34–38.
doi:10.1016/j.cub.2010.11.042
- Felician, O., Anton, J.-L., Nazarian, B., Roth, M., Roll, J.-P., & Romainière, P. (2009). Where is your shoulder? Neural correlates of localizing others' body parts. *Neuropsychologia*, *47*(8–9), 1909–1916. doi:10.1016/j.neuropsychologia.2009.03.001
- 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.
doi:10.1016/S0028-3932(03)00046-0
- Felician, O., & Romainière, P. (2008). Your body and mine: A neuropsychological perspective. *Neurophysiologie Clinique/Clinical Neurophysiology*, *38*(3), 183–187.
doi:10.1016/j.neucli.2008.02.003

- Ferrè, E. R., Bottini, G., Iannetti, G. D., & Haggard, P. (2013). The balance of feelings: Vestibular modulation of bodily sensations. *Cortex*, *49*(3), 748–758.
doi:10.1016/j.cortex.2012.01.012
- Fini, C., Cardini, F., Tajadura-Jiménez, A., Serino, A., & Tsakiris, M. (2013). Embodying an outgroup: The role of racial bias and the effect of multisensory processing in somatosensory remapping. *Frontiers in Behavioral Neuroscience*, *7*.
doi:10.3389/fnbeh.2013.00165
- Fiorio, M., & Haggard, P. (2005). Viewing the body prepares the brain for touch: Effects of TMS over somatosensory cortex. *European Journal of Neuroscience*, *22*(3), 773–777.
doi:10.1111/j.1460-9568.2005.04267.x
- Fisher, S. (1968). Body image. In D. L. Sills (Ed.), *International Encyclopedia of the Social Sciences*, *2* (pp. 113–116). New York: Free Press/Macmillan.
- Flor, H., Braun, C., Elbert, T., & Birbaumer, N. (1997). Extensive reorganization of primary somatosensory cortex in chronic back pain patients. *Neuroscience Letters*, *224*(1), 5–8.
doi:10.1016/S0304-3940(97)13441-3
- Flor, H., Denke, C., Schaefer, M., & Grüsser, S. (2001). Effect of sensory discrimination training on cortical reorganisation and phantom limb pain. *The Lancet*, *357*(9270), 1763–1764.
doi:10.1016/S0140-6736(00)04890-X
- Flor, H., Elbert, T., Knecht, S., Wienbruch, C., Pantev, C., Birbaumer, N., ... Taub, E. (1995). Phantom-limb pain as a perceptual correlate of cortical reorganization following arm amputation. *Nature*, *375*(6531), 482–484. doi:10.1038/375482a0
- Foltz, E. L., & White, L. E. (1962). Pain “relief” by frontal cingulumotomy. *Journal of Neurosurgery*, *19*(2), 89–100. doi:10.3171/jns.1962.19.2.0089
- Fox, C. J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research*, *1127*, 80–89. doi:10.1016/j.brainres.2006.09.104

- Fox, C. J., Oruç, I., & Barton, J. J. S. (2008). It doesn't matter how you feel. The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision*, *8*(3), 11.
doi:10.1167/8.3.11
- Frot, M., Magnin, M., Mauguière, F., & Garcia-Larrea, L. (2007). Human SII and posterior insula differently encode thermal laser stimuli. *Cerebral Cortex*, *17*(3), 610–620.
doi:10.1093/cercor/bhk007
- Gabriel, M., Kubota, Y., Sparenborg, S., Straube, K., & Vogt, B. A. (1991). Effects of cingulate cortical lesions on avoidance learning and training-induced unit activity in rabbits. *Experimental Brain Research*, *86*(3), 585–600. doi:10.1007/BF00230532
- Gallagher, S. (1986). Body image and body schema: A conceptual clarification. *Journal of Mind and Behavior*, *7*(4), 541–554.
- Gallagher, S., & Cole, J. (1995). Body image and body schema in a deafferented subject. *Journal of Mind and Behavior*, *16*(4), 369–389.
- Gallegos, D. R., & Tranel, D. (2005). Positive facial affect facilitates the identification of famous faces. *Brain and Language*, *93*(3), 338–348. doi:10.1016/j.bandl.2004.11.001
- Gallese, V. (2001). The “shared manifold” hypothesis. From mirror neurons to empathy. *Journal of Consciousness Studies*, *8*(5-6), 33–50.
- Gallup, G. G., Jr. (1970). Chimpanzees: Self-recognition. *Science*, *167*(3914), 86–87.
doi:10.1126/science.167.3914.86
- Gallup, G. G., Jr. (1977). Self recognition in primates: A comparative approach to the bidirectional properties of consciousness. *American Psychologist*, *32*(5), 329–338.
doi:10.1037/0003-066X.32.5.329
- Ganel, T., Valyear, K. F., Goshen-Gottstein, Y., & Goodale, M. A. (2005). The involvement of the “fusiform face area” in processing facial expression. *Neuropsychologia*, *43*(11), 1645–1654. doi:10.1016/j.neuropsychologia.2005.01.012

- Gao, Y.-J., Ren, W.-H., Zhang, Y.-Q., & Zhao, Z.-Q. (2004). Contributions of the anterior cingulate cortex and amygdala to pain- and fear-conditioned place avoidance in rats. *Pain, 110*(1–2), 343–353. doi:10.1016/j.pain.2004.04.030
- Garcia-Larrea, L. (2012). Insights gained into pain processing from patients with focal brain lesions. *Neuroscience Letters, 520*(2), 188–191. doi:10.1016/j.neulet.2012.05.007
- Garcia-Larrea, L. (2012). The posterior insular-opercular region and the search of a primary cortex for pain. *Neurophysiologie Clinique/Clinical Neurophysiology, 42*(5), 299–313. doi:10.1016/j.neucli.2012.06.001
- Garcia-Larrea, L., & Peyron, R. (2013). Pain matrices and neuropathic pain matrices: A review. *Pain, 154, Supplement 1*, S29–S43. doi:10.1016/j.pain.2013.09.001
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform “face area” is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12*(3), 495–504. doi:10.1162/089892900562165
- Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). Integration of visual and tactile signals from the hand in the human brain: An fMRI study. *Journal of Neurophysiology, 105*(2), 910–922. doi:10.1152/jn.00840.2010
- Gibson, J. (1966). *The Senses Considered as Perceptual Systems*. Boston, MA: Houghton Mifflin.
- Gingold, S. I., Greenspan, J. D., & Apkarian, A. V. (1991). Anatomic evidence of nociceptive inputs to primary somatosensory cortex: Relationship between spinothalamic terminals and thalamocortical cells in squirrel monkeys. *The Journal of Comparative Neurology, 308*(3), 467–490. doi:10.1002/cne.903080312
- Graziano, M. S. A., Cooke, D. F., & Taylor, C. S. R. (2000). Coding the location of the arm by sight. *Science, 290*(5497), 1782–1786. doi:10.1126/science.290.5497.1782
- Green, D. M., & Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. New York: John Wiley and Sons.

- Greenwald, A. G., & Banaji, M. R. (1995). Implicit social cognition: Attitudes, self-esteem, and stereotypes. *Psychological Review*, *102*(1), 4–27. doi:10.1037/0033-295X.102.1.4
- Grèzes, J., Costes, N., & Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain*, *122*(10), 1875–1887. doi:10.1093/brain/122.10.1875
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*, *7*(5), 555–562. doi:10.1038/nn1224
- Gross, J., Schnitzler, A., Timmermann, L., & Ploner, M. (2007). Gamma oscillations in human primary somatosensory cortex reflect pain perception. *PLoS Biology*, *5*(5), e133. doi:10.1371/journal.pbio.0050133
- Haggard, P. (2006). Just seeing you makes me feel better: Interpersonal enhancement of touch. *Social Neuroscience*, *1*(2), 104–110. doi:10.1080/17470910600976596
- Haggard, P., Christakou, A., & Serino, A. (2007). Viewing the body modulates tactile receptive fields. *Experimental Brain Research*, *180*(1), 187–193. doi:10.1007/s00221-007-0971-7
- Haggard, P., Iannetti, G. D., & Longo, M. R. (2013). Spatial sensory organization and body representation in pain perception. *Current Biology*, *23*(4), R164–R176. doi:10.1016/j.cub.2013.01.047
- Hamada, M., Murase, N., Hasan, A., Balaratnam, M., & Rothwell, J. C. (2013). The role of interneuron networks in driving human motor cortical plasticity. *Cerebral Cortex*, *23*(7), 1593–1605. doi:10.1093/cercor/bhs147
- Harmer, C. J., Thilo, K. V., Rothwell, J. C., & Goodwin, G. M. (2001). Transcranial magnetic stimulation of medial–frontal cortex impairs the processing of angry facial expressions. *Nature Neuroscience*, *4*(1), 17–18. doi:10.1038/82854

- Harris, J. A., Arabzadeh, E., Moore, C. A., & Clifford, C. W. G. (2007). Noninformative vision causes adaptive changes in tactile sensitivity. *The Journal of Neuroscience*, *27*(27), 7136–7140. doi:10.1523/JNEUROSCI.2102-07.2007
- Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, *32*(3), 203–218. doi:10.1016/S0166-4328(89)80054-3
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*(2), 301–307. doi:10.1016/S0896-6273(03)00838-9
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233. doi:10.1016/S1364-6613(00)01482-0
- Hayes, D. J., & Northoff, G. (2012). Common brain activations for painful and non-painful aversive stimuli. *BMC Neuroscience*, *13*(1), 60. doi:10.1186/1471-2202-13-60
- Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, *34*(2-3), 102–254. doi:10.1093/brain/34.2-3.102
- Henderson, L. A., Gandevia, S. C., & Macefield, V. G. (2007). Somatotopic organization of the processing of muscle and cutaneous pain in the left and right insula cortex: A single-trial fMRI study. *Pain*, *128*(1–2), 20–30. doi:10.1016/j.pain.2006.08.013
- Hodes, R. L., Rowland, E. W., Lightfoot, N., & Cleeland, C. S. (1990). The effects of distraction on responses to cold pressor pain. *Pain*, *41*(1), 109–114. doi:10.1016/0304-3959(90)91115-Y
- Hodzic, A., Kaas, A., Muckli, L., Stirn, A., & Singer, W. (2009). Distinct cortical networks for the detection and identification of human body. *NeuroImage*, *45*(4), 1264–1271. doi:10.1016/j.neuroimage.2009.01.027

- Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. *Human Brain Mapping, 30*(3), 951–962. doi:10.1002/hbm.20558
- Hofbauer, R. K., Rainville, P., Duncan, G. H., & Bushnell, M. C. (2001). Cortical representation of the sensory dimension of pain. *Journal of Neurophysiology, 86*(1), 402–411.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience, 3*(1), 80–84. doi:10.1038/71152
- Höfle, M., Hauck, M., Engel, A. K., & Senkowski, D. (2012). Viewing a needle pricking a hand that you perceive as yours enhances unpleasantness of pain. *Pain, 153*(5), 1074–1081. doi:10.1016/j.pain.2012.02.010
- Höfle, M., Pomper, U., Hauck, M., Engel, A. K., & Senkowski, D. (2013). Spectral signatures of viewing a needle approaching one's body when anticipating pain. *European Journal of Neuroscience, 38*(7), 3089–3098. doi:10.1111/ejn.12304
- Hornak, J., Rolls, E. T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia, 34*(4), 247–261. doi:10.1016/0028-3932(95)00106-9
- Huang, Y.-Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron, 45*(2), 201–206. doi:10.1016/j.neuron.2004.12.033
- Humphreys, K., Avidan, G., & Behrmann, M. (2007). A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia. *Experimental Brain Research, 176*(2), 356–373. doi:10.1007/s00221-006-0621-5
- Hutchison, W. D., Davis, K. D., Lozano, A. M., Tasker, R. R., & Dostrovsky, J. O. (1999). Pain-related neurons in the human cingulate cortex. *Nature Neuroscience, 2*(5), 403–405. doi:10.1038/8065

- Iannetti, G. D., Hughes, N. P., Lee, M. C., & Mouraux, A. (2008). Determinants of laser-evoked EEG responses: Pain perception or stimulus saliency? *Journal of Neurophysiology*, *100*(2), 815–828. doi:10.1152/jn.00097.2008
- Iannetti, G. D., & Mouraux, A. (2010). From the neuromatrix to the pain matrix (and back). *Experimental Brain Research*, *205*(1), 1–12. doi:10.1007/s00221-010-2340-1
- Iannetti, G. D., Zambreanu, L., Cruccu, G., & Tracey, I. (2005). Operculoinsular cortex encodes pain intensity at the earliest stages of cortical processing as indicated by amplitude of laser-evoked potentials in humans. *Neuroscience*, *131*(1), 199–208. doi:10.1016/j.neuroscience.2004.10.035
- IASP Task Force on Taxonomy. (1994). *Classification of Chronic Pain: Descriptions of Chronic Pain Syndromes and Definitions of Pain Terms*. (H. Merskey & N. Bogduk, Eds.) (2nd ed.). Seattle, WA: IASP Press.
- Inoue-Nakamura, N. (1997). Mirror self-recognition in nonhuman primates: A phylogenetic approach. *Japanese Psychological Research*, *39*(3), 266–275. doi:10.1111/1468-5884.00059
- Inui, K., Tsuji, T., & Kakigi, R. (2006). Temporal analysis of cortical mechanisms for pain relief by tactile stimuli in humans. *Cerebral Cortex*, *16*(3), 355–365. doi:10.1093/cercor/bhi114
- Ishai, A. (2008). Let's face it: It's a cortical network. *NeuroImage*, *40*(2), 415–419. doi:10.1016/j.neuroimage.2007.10.040
- Ishizu, T., Noguchi, A., Ito, Y., Ayabe, T., & Kojima, S. (2009). Motor activity and imagery modulate the body-selective region in the occipital–temporal area: A near-infrared spectroscopy study. *Neuroscience Letters*, *465*(1), 85–89. doi:10.1016/j.neulet.2009.08.079
- James, W. (1890). *The Principles of Psychology*. New York : Holt. Retrieved from <http://archive.org/details/theprinciplesofp01jameuoft>

- Johansen, J. P., Fields, H. L., & Manning, B. H. (2001). The affective component of pain in rodents: Direct evidence for a contribution of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences*, *98*(14), 8077–8082. doi:10.1073/pnas.141218998
- Kaas, J. H., Nelson, R. J., Sur, M., Lin, C. S., & Merzenich, M. M. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science*, *204*(4392), 521–523. doi:10.1126/science.107591
- Kammers, M. P. M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. *Neuropsychologia*, *47*(1), 204–211. doi:10.1016/j.neuropsychologia.2008.07.028
- Kammers, M. P. M., Verhagen, L., Dijkerman, H. C., Hogendoorn, H., de Vignemont, F., & Schutter, D. J. L. G. (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. doi:10.1162/jocn.2009.21095
- Kanazawa, S. (1996). Recognition of facial expressions in a Japanese monkey (*Macaca fuscata*) and humans (*Homo sapiens*). *Primates*, *37*(1), 25–38. doi:10.1007/BF02382917
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302–4311.
- Kanwisher, N., Stanley, D., & Harris, A. (1999). The fusiform face area is selective for faces not animals. *Neuroreport*, *10*(1), 183–187.
- Karnath, H.-O. (1997). Spatial orientation and the representation of space with parietal lobe lesions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *352*(1360), 1411–1419. doi:10.1098/rstb.1997.0127
- Keenan, J. P., Gallup, G. G., Jr., & Falk, D. (2003). *The Face in the Mirror: The Search for the Origins of Consciousness* (Vol. xxiii). New York: HarperCollins.

- Keenan, J. P., McCutcheon, B., Freund, S., Gallup, G. G., Jr., Sanders, G., & Pascual-Leone, A. (1999). Left hand advantage in a self-face recognition task. *Neuropsychologia*, *37*(12), 1421–1425. doi:10.1016/S0028-3932(99)00025-1
- Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology*, *11*(15), 1188–1191. doi:10.1016/S0960-9822(01)00327-X
- Kenshalo, D. R., Jr., Chudler, E. H., Anton, F., & Dubner, R. (1988). SI nociceptive neurons participate in the encoding process by which monkeys perceive the intensity of noxious thermal stimulation. *Brain Research*, *454*(1–2), 378–382. doi:10.1016/0006-8993(88)90841-4
- Kenshalo, D. R., Jr., Giesler, G. J., Leonard, R. B., & Willis, W. D. (1980). Responses of neurons in primate ventral posterior lateral nucleus to noxious stimuli. *Journal of Neurophysiology*, *43*(6), 1594–1614.
- Kenshalo, D. R., Jr., & Isensee, O. (1983). Responses of primate SI cortical neurons to noxious stimuli. *Journal of Neurophysiology*, *50*(6), 1479–1496.
- Keyes, H., & Brady, N. (2010). Self-face recognition is characterized by “bilateral gain” and by faster, more accurate performance which persists when faces are inverted. *The Quarterly Journal of Experimental Psychology*, *63*(5), 840–847. doi:10.1080/17470211003611264
- Keyes, H., Brady, N., Reilly, R. B., & Foxe, J. J. (2010). My face or yours? Event-related potential correlates of self-face processing. *Brain and Cognition*, *72*(2), 244–254. doi:10.1016/j.bandc.2009.09.006
- Keysers, C., Wicker, B., Gazzola, V., Anton, J.-L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, *42*(2), 335–346. doi:10.1016/S0896-6273(04)00156-4

- Kitada, R., Johnsrude, I. S., Kochiyama, T., & Lederman, S. J. (2009). Functional specialization and convergence in the occipito-temporal cortex supporting haptic and visual identification of human faces and body parts: An fMRI study. *Journal of Cognitive Neuroscience*, *21*(10), 2027–2045. doi:10.1162/jocn.2009.21115
- Kolb, L. C. (1959). The body image in the schizophrenic reaction. In A. Auerback (Ed.), *Schizophrenia: An Integrated Approach* (pp. 87–97). New York: Ronald Press.
- Konen, C. S., & Haggard, P. (2014). Multisensory parietal cortex contributes to visual enhancement of touch in humans: A single-pulse TMS study. *Cerebral Cortex*, *24*(2), 501–507. doi:10.1093/cercor/bhs331
- Konen, C. S., & Kastner, S. (2008). Representation of eye movements and stimulus motion in topographically organized areas of human posterior parietal cortex. *The Journal of Neuroscience*, *28*(33), 8361–8375. doi:10.1523/JNEUROSCI.1930-08.2008
- Kong, J., White, N. S., Kwong, K. K., Vangel, M. G., Rosman, I. S., Gracely, R. H., & Gollub, R. L. (2006). Using fMRI to dissociate sensory encoding from cognitive evaluation of heat pain intensity. *Human Brain Mapping*, *27*(9), 715–721. doi:10.1002/hbm.20213
- Kottoor, T. M. (1989). Recognition of faces by adults. *Psychological Studies*, *34*(2), 102–105.
- Koyama, T., Kato, K., & Mikami, A. (2000). During pain-avoidance neurons activated in the macaque anterior cingulate and caudate. *Neuroscience Letters*, *283*(1), 17–20. doi:10.1016/S0304-3940(00)00894-6
- Koyama, T., Kato, K., Tanaka, Y. Z., & Mikami, A. (2001). Anterior cingulate activity during pain-avoidance and reward tasks in monkeys. *Neuroscience Research*, *39*(4), 421–430. doi:10.1016/S0168-0102(01)00197-3
- Koyama, T., Tanaka, Y. Z., & Mikami, A. (1998). Nociceptive neurons in the macaque anterior cingulate activate during anticipation of pain. *Neuroreport*, *9*(11), 2663–2667.

- Kujala, M. V., Kujala, J., Carlson, S., & Hari, R. (2012). Dog experts' brains distinguish socially relevant body postures similarly in dogs and humans. *PLoS ONE*, *7*(6), e39145.
doi:10.1371/journal.pone.0039145
- Kumazawa, T., & Perl, E. R. (1978). Excitation of marginal and substantia gelatinosa neurons in the primate spinal cord: Indications of their place in dorsal horn functional organization. *The Journal of Comparative Neurology*, *177*(3), 417–434. doi:10.1002/cne.901770305
- LaBar, K. S., LeDoux, J. E., Spencer, D. D., & Phelps, E. A. (1995). Impaired fear conditioning following unilateral temporal lobectomy in humans. *The Journal of Neuroscience*, *15*(10), 6846–6855.
- LaGraize, S. C., Labuda, C. J., Rutledge, M. A., Jackson, R. L., & Fuchs, P. N. (2004). Differential effect of anterior cingulate cortex lesion on mechanical hypersensitivity and escape/avoidance behavior in an animal model of neuropathic pain. *Experimental Neurology*, *188*(1), 139–148. doi:10.1016/j.expneurol.2004.04.003
- Laskin, S. E., & Spencer, W. A. (1979). Cutaneous masking. I. Psychophysical observations on interactions of multipoint stimuli in man. *Journal of Neurophysiology*, *42*(4), 1048–1060.
- Lefaucheur, J. P., Drouot, X., Ménard-Lefaucheur, I., Keravel, Y., & Nguyen, J. P. (2006). Motor cortex rTMS restores defective intracortical inhibition in chronic neuropathic pain. *Neurology*, *67*(9), 1568–1574. doi:10.1212/01.wnl.0000242731.10074.3c
- Legrain, V., Iannetti, G. D., Plaghki, L., & Mouraux, A. (2011). The pain matrix reloaded: A salience detection system for the body. *Progress in Neurobiology*, *93*(1), 111–124.
doi:10.1016/j.pneurobio.2010.10.005
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, *317*(5841), 1096–1099.
doi:10.1126/science.1143439

- Lenz, M., Höffken, O., Stude, P., Lissek, S., Schwenkreis, P., Reinersmann, A., ... Maier, C. (2011). Bilateral somatosensory cortex disinhibition in complex regional pain syndrome type I. *Neurology*, *77*(11), 1096–1101. doi:10.1212/WNL.0b013e31822e1436
- Le Pera, D., Graven-Nielsen, T., Valeriani, M., Oliviero, A., Di Lazzaro, V., Tonali, P. A., & Arendt-Nielsen, L. (2001). Inhibition of motor system excitability at cortical and spinal level by tonic muscle pain. *Clinical Neurophysiology*, *112*(9), 1633–1641. doi:10.1016/S1388-2457(01)00631-9
- Levine, D. N., Kaufman, K. J., & Mohr, J. P. (1978). Inaccurate reaching associated with a superior parietal lobe tumor. *Neurology*, *28*(6), 556–556. doi:10.1212/WNL.28.6.556
- Levine, J. D., Gordon, N. C., Smith, R., & Fields, H. L. (1982). Post-operative pain: Effect of extent of injury and attention. *Brain Research*, *234*(2), 500–504.
- Light, A. R., & Perl, E. R. (1979). Spinal termination of functionally identified primary afferent neurons with slowly conducting myelinated fibers. *The Journal of Comparative Neurology*, *186*(2), 133–150. doi:10.1002/cne.901860203
- Liu, J., Harris, A., & Kanwisher, N. (2010). Perception of face parts and face configurations: An fMRI study. *Journal of Cognitive Neuroscience*, *22*(1), 203–211. doi:10.1162/jocn.2009.21203
- Lockwood, P. L., Iannetti, G. D., & Haggard, P. (2013). Transcranial magnetic stimulation over human secondary somatosensory cortex disrupts perception of pain intensity. *Cortex*, *49*(8), 2201–2209. doi:10.1016/j.cortex.2012.10.006
- Longo, M. R., Betti, V., Aglioti, S. M., & Haggard, P. (2009). Visually induced analgesia: Seeing the body reduces pain. *The Journal of Neuroscience*, *29*(39), 12125–12130. doi:10.1523/JNEUROSCI.3072-09.2009
- Longo, M. R., Iannetti, G. D., Mancini, F., Driver, J., & Haggard, P. (2012). Linking pain and the body: Neural correlates of visually induced analgesia. *The Journal of Neuroscience*, *32*(8), 2601–2607. doi:10.1523/JNEUROSCI.4031-11.2012

- Lötsch, J., Walter, C., Felden, L., Nöth, U., Deichmann, R., & Oertel, B. G. (2012). The human operculo-insular cortex is pain-preferentially but not pain-exclusively activated by trigeminal and olfactory stimuli. *PLoS ONE*, *7*(4), e34798.
doi:10.1371/journal.pone.0034798
- Mackay, W. A., & Crammond, D. J. (1987). Neuronal correlates in posterior parietal lobe of the expectation of events. *Behavioural Brain Research*, *24*(3), 167–179. doi:10.1016/0166-4328(87)90055-6
- Macmillan, N. A., & Kaplan, H. L. (1985). Detection theory analysis of group data: Estimating sensitivity from average hit and false-alarm rates. *Psychological Bulletin*, *98*(1), 185–199. doi:10.1037/0033-2909.98.1.185
- Maihöfner, C., Handwerker, H. O., Neundörfer, B., & Birklein, F. (2003). Patterns of cortical reorganization in complex regional pain syndrome. *Neurology*, *61*(12), 1707–1715.
doi:10.1212/01.WNL.0000098939.02752.8E
- Maister, L., Tsiakkas, E., & Tsakiris, M. (2013). I feel your fear: Shared touch between faces facilitates recognition of fearful facial expressions. *Emotion*, *13*(1), 7–13.
doi:10.1037/a0030884
- 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. doi:10.1523/JNEUROSCI.3653-06.2007
- Mancini, F., Bolognini, N., Haggard, P., & Vallar, G. (2012). tDCS modulation of visually induced analgesia. *Journal of Cognitive Neuroscience*, *24*(12), 2419–2427.
doi:10.1162/jocn_a_00293
- Mancini, F., Haggard, P., Iannetti, G. D., Longo, M. R., & Sereno, M. I. (2012). Fine-grained nociceptive maps in primary somatosensory cortex. *The Journal of Neuroscience*, *32*(48), 17155–17162. doi:10.1523/JNEUROSCI.3059-12.2012

- Mancini, F., Longo, M. R., Canzoneri, E., Vallar, G., & Haggard, P. (2013). Changes in cortical oscillations linked to multisensory modulation of nociception. *European Journal of Neuroscience*, *37*(5), 768–776. doi:10.1111/ejn.12080
- Mancini, F., Longo, M. R., Kammers, M. P. M., & Haggard, P. (2011). Visual distortion of body size modulates pain perception. *Psychological Science*, *22*(3), 325–330. doi:10.1177/0956797611398496
- Mancini, F., Nash, T., Iannetti, G. D., & Haggard, P. (2014). Pain relief by touch: A quantitative approach. *Pain*, *155*(3), 635–642. doi:10.1016/j.pain.2013.12.024
- Marino, L., Reiss, D., & Gallup, G. G., Jr. (1994). Mirror self-recognition in bottlenose dolphins: Implications for comparative investigations of highly dissimilar species. In S. T. Parker, R. W. Mitchell, & M. L. Boccia (Eds.), *Self-Awareness in Animals and Humans: Developmental Perspectives* (pp. 380–391). New York: Cambridge University Press.
- Mazzola, L., Faillenot, I., Barral, F.-G., Mauguière, F., & Peyron, R. (2012). Spatial segregation of somato-sensory and pain activations in the human operculo-insular cortex. *NeuroImage*, *60*(1), 409–418. doi:10.1016/j.neuroimage.2011.12.072
- Mazzola, L., Isnard, J., Peyron, R., Guénot, M., & Mauguière, F. (2009). Somatotopic organization of pain responses to direct electrical stimulation of the human insular cortex. *Pain*, *146*(1–2), 99–104. doi:10.1016/j.pain.2009.07.014
- Mazzola, L., Isnard, J., Peyron, R., & Mauguière, F. (2012). Stimulation of the human cortex and the experience of pain: Wilder Penfield's observations revisited. *Brain*, *135*, 631-640. doi:10.1093/brain/awr265
- Mazurega, M., Pavani, F., Paladino, M. P., & Schubert, T. W. (2011). Self-other bodily merging in the context of synchronous but arbitrary-related multisensory inputs. *Experimental Brain Research*, *213*(2-3), 213–221. doi:10.1007/s00221-011-2744-6

- McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex*, *9*(5), 431–444. doi:10.1093/cercor/9.5.431
- Melzack, R., & Casey, K. L. (1968). Sensory, motivational and central control determinants of pain: A new conceptual model. In D. R. Kenshalo, Jr. (Ed.), *The Skin Senses* (pp. 423–443). Springfield, IL: C. C. Thomas.
- Merleau-Ponty, M. (1962). *Phenomenology of Perception*. London: Routledge.
- Meulders, A., Vansteenwegen, D., & Vlaeyen, J. W. S. (2012). Women, but not men, report increasingly more pain during repeated (un)predictable painful electrocutaneous stimulation: Evidence for mediation by fear of pain. *Pain*, *153*(5), 1030–1041. doi:10.1016/j.pain.2012.02.005
- Miron, D., Duncan, G. H., & Bushnell, M. C. (1989). Effects of attention on the intensity and unpleasantness of thermal pain. *Pain*, *39*(3), 345–352. doi:10.1016/0304-3959(89)90048-1
- Mochizuki, H., Sadato, N., Saito, D. N., Toyoda, H., Tashiro, M., Okamura, N., & Yanai, K. (2007). Neural correlates of perceptual difference between itching and pain: A human fMRI study. *NeuroImage*, *36*(3), 706–717. doi:10.1016/j.neuroimage.2007.04.003
- Mohan, R., Jensen, K. B., Petkova, V. I., Dey, A., Barnsley, N., Ingvar, M., ... Ehrsson, H. H. (2012). No pain relief with the rubber hand illusion. *PLoS ONE*, *7*(12), e52400. doi:10.1371/journal.pone.0052400
- Mondloch, C. J., Geldart, S., Maurer, D., & Grand, R. L. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology*, *86*(1), 67–84. doi:10.1016/S0022-0965(03)00102-4
- Morris, J. S., & Dolan, R. J. (2001). Involvement of human amygdala and orbitofrontal cortex in hunger-enhanced memory for food stimuli. *The Journal of Neuroscience*, *21*(14), 5304–5310.

- Morris, J. S., Friston, K. J., Büchel, C., Frith, C. D., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*(1), 47–57. doi:10.1093/brain/121.1.47
- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*(6603), 812–815. doi:10.1038/383812a0
- Morrison, I., Lloyd, D., di Pellegrino, G., & Roberts, N. (2004). Vicarious responses to pain in anterior cingulate cortex: Is empathy a multisensory issue? *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 270–278. doi:10.3758/CABN.4.2.270
- Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences*, *105*(35), 13169–13173. doi:10.1073/pnas.0803768105
- Moseley, G. L., & Wiech, K. (2009). The effect of tactile discrimination training is enhanced when patients watch the reflected image of their unaffected limb during training. *Pain*, *144*(3), 314–319. doi:10.1016/j.pain.2009.04.030
- Moseley, G. L., Zalucki, N. M., & Wiech, K. (2008). Tactile discrimination, but not tactile stimulation alone, reduces chronic limb pain. *Pain*, *137*(3), 600–608. doi:10.1016/j.pain.2007.10.021
- Mountcastle, V. B. (1984). Central nervous mechanisms in mechanoreceptive sensibility. In R. Terjung (Ed.), *Comprehensive Physiology*. Hoboken, NJ: John Wiley & Sons, Inc.
- Retrieved from <http://www.comprehensivephysiology.com/WileyCDA/CompPhysArticle/refId-cp010318.html>

- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, *38*(4), 871–908.
- Mouraux, A., Diukova, A., Lee, M. C., Wise, R. G., & Iannetti, G. D. (2011). A multisensory investigation of the functional significance of the “pain matrix.” *NeuroImage*, *54*(3), 2237–2249. doi:10.1016/j.neuroimage.2010.09.084
- Mouraux, A., & Iannetti, G. D. (2009). Nociceptive laser-evoked brain potentials do not reflect nociceptive-specific neural activity. *Journal of Neurophysiology*, *101*(6), 3258–3269. doi:10.1152/jn.91181.2008
- Mouraux, A., & Plaghki, L. (2007). Cortical interactions and integration of nociceptive and non-nociceptive somatosensory inputs in humans. *Neuroscience*, *150*(1), 72–81. doi:10.1016/j.neuroscience.2007.08.035
- Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. *NeuroImage*, *42*(4), 1669–1677. doi:10.1016/j.neuroimage.2008.05.045
- Myers, G. (1967). Self and body-image. In J. M. Edie (Ed.), *Phenomenology in America* (pp. 147–60). Chicago, IL: Quadrangle Books.
- Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., ... Kojima, S. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neurophysiology*, *82*(3), 1610–1614.
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, *12*(2), 225–231. doi:10.1016/S0926-6410(01)00053-2
- Neiworth, J. J., Hassett, J. M., & Sylvester, C. J. (2007). Face processing in humans and new world monkeys: The influence of experiential and ecological factors. *Animal Cognition*, *10*(2), 125–134. doi:10.1007/s10071-006-0045-4

- Nichols, D. F., Betts, L. R., & Wilson, H. R. (2010). Decoding of faces and face components in face-sensitive human visual cortex. *Perception Science*, 1, 28.
doi:10.3389/fpsyg.2010.00028
- Nielsen, M. (1938). Gerstmann syndrome: Finger agnosia, agraphia, confusion of right and left and acalculia: Comparison of this syndrome with disturbance of body scheme resulting from lesions of the right side of the brain. *Archives of Neurology & Psychiatry*, 39(3), 536–560. doi:10.1001/archneurpsyc.1938.02270030114009
- Nielsen, M., & Dissanayake, C. (2004). Pretend play, mirror self-recognition and imitation: A longitudinal investigation through the second year. *Infant Behavior and Development*, 27(3), 342–365. doi:10.1016/j.infbeh.2003.12.006
- Nielsen, M., Suddendorf, T., & Slaughter, V. (2006). Mirror self-recognition beyond the face. *Child Development*, 77(1), 176–185. doi:10.1111/j.1467-8624.2006.00863.x
- Ogden, J. A. (1985). Autotopagnosia. *Brain*, 108(4), 1009–1022. doi:10.1093/brain/108.4.1009
- Ohara, S., Crone, N. E., Weiss, N., Treede, R.-D., & Lenz, F. A. (2004). Amplitudes of laser evoked potential recorded from primary somatosensory, parasyylvian and medial frontal cortex are graded with stimulus intensity. *Pain*, 110(1–2), 318–328.
doi:10.1016/j.pain.2004.04.009
- Orlov, T., Makin, T. R., & Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron*, 68(3), 586–600. doi:10.1016/j.neuron.2010.09.032
- O’Shaughnessy, B. (1995). Proprioception and the body image. In J. L. Bermudez, A. J. Marcel, & N. M. Eilan (Eds.), *The Body and the Self* (pp. 175-204). Cambridge, MA: MIT Press.
- 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. 197-214). Sofia, Bulgaria: Academic Publishing House.

- Paladino, M.-P., Mazzurega, M., Pavani, F., & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. *Psychological Science*, 21(9), 1202–1207. doi:10.1177/0956797610379234
- Pascalis, O., & Bachevalier, J. (1998). Face recognition in primates: A cross-species study. *Behavioural Processes*, 43(1), 87–96. doi:10.1016/S0376-6357(97)00090-9
- Pascalis, O., de Haan, M., & Nelson, C. A. (2002). Is face processing species-specific during the first year of life? *Science*, 296(5571), 1321–1323. doi:10.1126/science.1070223
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608. doi:10.1152/jn.00513.2004
- Penfield, W., & Rasmussen, T. (1950). *The Cerebral Cortex of Man; A Clinical Study of Localization of Function* (Vol. xv). Oxford, UK: Macmillan.
- Perl, E. R. (1968). Myelinated afferent fibres innervating the primate skin and their response to noxious stimuli. *The Journal of Physiology*, 197(3), 593–615.
- Perrett, D. I., Hietanen, J. K., Oram, M. W., Benson, P. J., & Rolls, E. T. (1992). Organization and functions of cells responsive to faces in the temporal cortex [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 335(1273), 23–30. doi:10.1098/rstb.1992.0003
- Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS ONE*, 3(12), e3832. doi:10.1371/journal.pone.0003832
- Peyron, R., Laurent, B., & García-Larrea, L. (2000). Functional imaging of brain responses to pain. A review and meta-analysis (2000). *Neurophysiologie Clinique/Clinical Neurophysiology*, 30(5), 263–288. doi:10.1016/S0987-7053(00)00227-6
- Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., ... Gray, J. A. (1998). Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society of London B: Biological Sciences*, 265(1408), 1809–1817. doi:10.1098/rspb.1998.0506

- Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., ... David, A. S. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature*, 389(6650), 495–498. doi:10.1038/39051
- Pichon, S., de Gelder, B., & Grèzes, J. (2009). Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *NeuroImage*, 47(4), 1873–1883. doi:10.1016/j.neuroimage.2009.03.084
- Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology*, 19(4), 319–324. doi:10.1016/j.cub.2009.01.007
- Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research*, 209(4), 481–493. doi:10.1007/s00221-011-2579-1
- Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology*, 17(18), 1568–1573. doi:10.1016/j.cub.2007.07.063
- Plotnik, J. M., de Waal, F. B. M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences*, 103(45), 17053–17057. doi:10.1073/pnas.0608062103
- Pourtois, G., Sander, D., Andres, M., Grandjean, D., Reveret, L., Olivier, E., & Vuilleumier, P. (2004). Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. *European Journal of Neuroscience*, 20(12), 3507–3515. doi:10.1111/j.1460-9568.2004.03794.x
- Press, C., Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Visual enhancement of touch in spatial body representation. *Experimental Brain Research*, 154(2), 238–245. doi:10.1007/s00221-003-1651-x

- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology*, *6*(8), e202.
doi:10.1371/journal.pbio.0060202
- Racca, A., Guo, K., Meints, K., & Mills, D. S. (2012). Reading faces: Differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *PLoS ONE*, *7*(4), e36076. doi:10.1371/journal.pone.0036076
- Rainville, P., Duncan, G. H., Price, D. D., Carrier, B., & Bushnell, M. C. (1997). Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science*, *277*(5328), 968–971. doi:10.1126/science.277.5328.968
- Rausell, E., & Jones, E. G. (1991). Histochemical and immunocytochemical compartments of the thalamic VPM nucleus in monkeys and their relationship to the representational map. *The Journal of Neuroscience*, *11*(1), 210–225.
- Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences*, *98*(10), 5937–5942. doi:10.1073/pnas.101086398
- Rhudy, J. L., & Meagher, M. W. (2000). Fear and anxiety: Divergent effects on human pain thresholds. *Pain*, *84*(1), 65–75. doi:10.1016/S0304-3959(99)00183-9
- Roland, P. E. (1987). Somatosensory detection of microgeometry, macrogeometry and kinesthesia after localized lesions of the cerebral hemispheres in man. *Brain Research Reviews*, *12*(1), 43–94. doi:10.1016/0165-0173(87)90018-X
- Rollman, G. B. (1977). Signal detection theory measurement of pain: A review and critique. *Pain*, *3*(3), 187–211. doi:10.1016/0304-3959(77)90002-1
- Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., & The Safety of TMS Consensus Group. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, *120*(12), 2008–2039. doi:10.1016/j.clinph.2009.08.016

- Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, 8(1), 107–113. doi:10.1038/nn1370
- Ro, T., Wallace, R., Hagedorn, J., Farné, A., & Pienkos, E. (2004). Visual enhancing of tactile perception in the posterior parietal cortex. *Journal of Cognitive Neuroscience*, 16(1), 24–30. doi:10.1162/089892904322755520
- Sakata, H., Takaoka, Y., Kawarasaki, A., & Shibutani, H. (1973). Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Research*, 64, 85–102. doi:10.1016/0006-8993(73)90172-8
- Sansone, S., & Tiberghien, G. (1994). Facial expression coding and face recognition: Independent or interactive processes. *Psychologie Francaise*, 39(4), 327–343.
- Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. *Cerebral Cortex*, 16(2), 178–182. doi:10.1093/cercor/bhi095
- Schaefer, M., Heinze, H.-J., & Rotte, M. (2005). Seeing the hand being touched modulates the primary somatosensory cortex. *Neuroreport*, 16(10), 1101–1105.
- Schaefer, M., Xu, B., Flor, H., & Cohen, L. G. (2009). Effects of different viewing perspectives on somatosensory activations during observation of touch. *Human Brain Mapping*, 30(9), 2722–2730. doi:10.1002/hbm.20701
- Schilder, P. (1923). *Das Körperschema: Ein Beitrag zur Lehre vom Bewusstsein des eigenen Körpers*. Berlin: Julius Springer.
- Schilder, P. (1935). *The Image and Appearance of the Human Body*. Oxford, UK: Kegan Paul.
- Schlack, A., Hoffmann, K.-P., & Bremmer, F. (2002). Interaction of linear vestibular and visual stimulation in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, 16(10), 1877–1886. doi:10.1046/j.1460-9568.2002.02251.x

- Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K.-P., & Bremmer, F. (2005). Multisensory space representations in the macaque ventral intraparietal area. *The Journal of Neuroscience*, *25*(18), 4616–4625. doi:10.1523/JNEUROSCI.0455-05.2005
- Schlereth, T., Baumgärtner, U., Magerl, W., Stoeter, P., & Treede, R.-D. (2003). Left-hemisphere dominance in early nociceptive processing in the human parasyllian cortex. *NeuroImage*, *20*(1), 441–454. doi:10.1016/S1053-8119(03)00345-8
- Schubert, T. W., & Otten, S. (2002). Overlap of self, ingroup, and outgroup: Pictorial measures of self-categorization. *Self and Identity*, *1*(4), 353–376.
doi:10.1080/152988602760328012
- Schweinberger, S. R., & Soukup, G. R. (1998). Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(6), 1748–1765.
- Schwenkreis, P., Janssen, F., Rommel, O., Pleger, B., Völker, B., Hosbach, I., ... Tegenthoff, M. (2003). Bilateral motor cortex disinhibition in complex regional pain syndrome (CRPS) type I of the hand. *Neurology*, *61*(4), 515–519. doi:10.1212/WNL.61.4.515
- Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, *17*(4), 543–553.
doi:10.1162/0898929053467587
- Scott, L. S., Shannon, R. W., & Nelson, C. A. (2005). Behavioral and electrophysiological evidence of species-specific face processing. *Cognitive, Affective, & Behavioral Neuroscience*, *5*(4), 405–416. doi:10.3758/CABN.5.4.405
- Scott, L. S., Shannon, R. W., & Nelson, C. A. (2006). Neural correlates of human and monkey face processing in 9-month-old infants. *Infancy*, *10*(2), 171–186.
doi:10.1207/s15327078in1002_4

- Sergent, J., Ohta, S., Macdonald, B., & Zuck, E. (1994). Segregated processing of facial identity and emotion in the human brain: A PET study. *Visual Cognition*, 1(2-3), 349–369. doi:10.1080/13506289408402305
- Sergent, J., & Villemure, J.-G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain*, 112(4), 975–995. doi:10.1093/brain/112.4.975
- Serino, A., Farnè, A., Rinaldesi, M. L., Haggard, P., & Làdavas, E. (2007). Can vision of the body ameliorate impaired somatosensory function? *Neuropsychologia*, 45(5), 1101–1107. doi:10.1016/j.neuropsychologia.2006.09.013
- Serino, A., Giovagnoli, G., & Làdavas, E. (2009). I feel what you feel if you are similar to me. *PLoS ONE*, 4(3), e4930. doi:10.1371/journal.pone.0004930
- Serino, A., Padiglioni, S., Haggard, P., & Làdavas, E. (2009). Seeing the hand boosts feeling on the cheek. *Cortex*, 45(5), 602–609. doi:10.1016/j.cortex.2008.03.008
- Serino, A., Pizzoferrato, F., & Làdavas, E. (2008). Viewing a face (especially one's own face) being touched enhances tactile perception on the face. *Psychological Science*, 19(5), 434–438. doi:10.1111/j.1467-9280.2008.02105.x
- 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(2), 148–162. doi:10.1080/17470910903205503
- Sikes, R. W., & Vogt, B. A. (1992). Nociceptive neurons in area 24 of rabbit cingulate cortex. *Journal of Neurophysiology*, 68(5), 1720–1732.
- Simmons, W. K., Avery, J. A., Barcalow, J. C., Bodurka, J., Drevets, W. C., & Bellgowan, P. (2013). Keeping the body in mind: Insula functional organization and functional connectivity integrate interoceptive, exteroceptive, and emotional awareness. *Human Brain Mapping*, 34(11), 2944–2958. doi:10.1002/hbm.22113

- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, *303*(5661), 1157–1162. doi:10.1126/science.1093535
- Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. *Brain*, *114*(1), 629–642. doi:10.1093/brain/114.1.629
- 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. doi:10.1371/journal.pone.0010564
- Sonnby–Borgström, M. (2002). Automatic mimicry reactions as related to differences in emotional empathy. *Scandinavian Journal of Psychology*, *43*(5), 433–443. doi:10.1111/1467-9450.00312
- Spangler, S. M., Schwarzer, G., Korell, M., & Maier-Karius, J. (2010). The relationships between processing facial identity, emotional expression, facial speech, and gaze direction during development. *Journal of Experimental Child Psychology*, *105*(1–2), 1–19. doi:10.1016/j.jecp.2009.09.003
- Spitoni, G. F., Galati, G., Antonucci, G., Haggard, P., & Pizzamiglio, L. (2010). Two forms of touch perception in the human brain. *Experimental Brain Research*, *207*(3-4), 185–195. doi:10.1007/s00221-010-2446-5
- Spitoni, G. F., Pireddu, G., Cimmino, R. L., Galati, G., Priori, A., Lavidor, M., ... Pizzamiglio, L. (2013). Right but not left angular gyrus modulates the metric component of the mental body representation: A tDCS study. *Experimental Brain Research*, *228*(1), 63–72. doi:10.1007/s00221-013-3538-9
- Sprenkelmeyer, R., Rausch, M., Eysel, U. T., & Przuntek, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings of the*

- Royal Society of London B: Biological Sciences*, 265(1409), 1927–1931.
doi:10.1098/rspb.1998.0522
- Sprenghelmeyer, R., Young, A. W., Schroeder, U., Grossenbacher, P. G., Federlein, J., Buttner, T., & Przuntek, H. (1999). Knowing no fear. *Proceedings of the Royal Society of London B: Biological Sciences*, 266(1437), 2451–2456. doi:10.1098/rspb.1999.0945
- Stoleru, S., Gregoire, M.-C., Gerard, D., Decety, J., Lafarge, E., Cinotti, L., ... Comar, D. (1999). Neuroanatomical correlates of visually evoked sexual arousal in human males. *Archives of Sexual Behavior*, 28(1), 1–21. doi:10.1023/A:1018733420467
- Straus, E. W. (1970). The phantom limb. In E. W. Straus & R. M. Griffith (Eds.), *Aisthesis and Aesthetics* (pp. 130-148). Pittsburgh, PA: Duquesne University Press.
- Suarez, S. D., & Gallup, G. G., Jr. (1981). Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution*, 10(2), 175–188. doi:10.1016/S0047-2484(81)80016-4
- Suddendorf, T., & Butler, D. L. (2013). The nature of visual self-recognition. *Trends in Cognitive Sciences*, 17(3), 121–127. doi:10.1016/j.tics.2013.01.004
- Sugiura, Y., Lee, C. L., & Perl, E. R. (1986). Central projections of identified, unmyelinated (C) afferent fibers innervating mammalian skin. *Science*, 234(4774), 358–361.
doi:10.1126/science.3764416
- Sui, J., & Han, S. (2007). Self-construal priming modulates neural substrates of self-awareness. *Psychological Science*, 18(10), 861–866. doi:10.1111/j.1467-9280.2007.01992.x
- Sui, J., Zhu, Y., & Han, S. (2006). Self-face recognition in attended and unattended conditions: An event-related brain potential study. *NeuroReport*, 17(4), 423–427.
doi:10.1097/01.wnr.0000203357.65190.61
- Tajadura-Jiménez, A., Grehl, S., & Tsakiris, M. (2012). The other in me: Interpersonal multisensory stimulation changes the mental representation of the self. *PLoS ONE*, 7(7), e40682. doi:10.1371/journal.pone.0040682

- Tajadura-Jiménez, A., Longo, M. R., Coleman, R., & Tsakiris, M. (2012). The person in the mirror: Using the enfacement illusion to investigate the experiential structure of self-identification. *Consciousness and Cognition*, *21*(4), 1725–1738.
doi:10.1016/j.concog.2012.10.004
- Tajadura-Jiménez, A., Lorusso, L., & Tsakiris, M. (2013). Active and passive-touch during interpersonal multisensory stimulation change self–other boundaries. *Consciousness and Cognition*, *22*(4), 1352–1360. doi:10.1016/j.concog.2013.09.002
- Tajadura-Jiménez, A., & Tsakiris, M. (2014). Balancing the “inner” and the “outer” self: Interoceptive sensitivity modulates self–other boundaries. *Journal of Experimental Psychology: General*, *143*(2), 736–744. doi:10.1037/a0033171
- Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Current Biology*, *12*(3), 233–236. doi:10.1016/S0960-9822(01)00681-9
- Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Persistence of visual–tactile enhancement in humans. *Neuroscience Letters*, *354*(1), 22–25. doi:10.1016/j.neulet.2003.09.068
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, *98*(3), 1626–1633. doi:10.1152/jn.00012.2007
- Tecchio, F., Padua, L., Aprile, I., & Rossini, P. M. (2002). Carpal tunnel syndrome modifies sensory hand cortical somatotopy: A MEG study. *Human Brain Mapping*, *17*(1), 28–36.
doi:10.1002/hbm.10049
- Tiemersma, D. (1982). “Body-image” and “body-schema” in the existential phenomenology of Merleau-Ponty. *Journal of the British Society of Phenomenology*, *13*, 246–255.
- Timmermann, L., Ploner, M., Haucke, K., Schmitz, F., Baltissen, R., & Schnitzler, A. (2001). Differential coding of pain intensity in the human primary and secondary somatosensory cortex. *Journal of Neurophysiology*, *86*(3), 1499–1503.

- Tipper, S. P., Lloyd, D., Shorland, B., Dancer, C., Howard, L. A., & McGlone, F. (1998). Vision influences tactile perception without proprioceptive orienting. *Neuroreport*, *9*(8), 1741–1744.
- Tong, F., & Nakayama, K. (1999). Robust representations for faces: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1016–1035. doi:10.1037/0096-1523.25.4.1016
- Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. (2000). Response properties of the human fusiform face area. *Cognitive Neuropsychology*, *17*(1-3), 257–280. doi:10.1080/026432900380607
- Tranel, D., Damasio, A. R., & Damasio, H. (1988). Intact recognition of facial expression, gender, and age in patients with impaired recognition of face identity. *Neurology*, *38*(5), 690–690. doi:10.1212/WNL.38.5.690
- Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PLoS ONE*, *3*(12), e4040. doi:10.1371/journal.pone.0004040
- Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703–712. doi:10.1016/j.neuropsychologia.2009.09.034
- Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: Multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, *204*(3), 343–352. doi:10.1007/s00221-009-2039-3
- Tsakiris, M., Costantini, M., & Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia*, *46*(12), 3014–3018. doi:10.1016/j.neuropsychologia.2008.06.004
- Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology*, *31*(1), 80–91.

- Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*, *17*(10), 2235–2244. doi:10.1093/cercor/bhl131
- Uddin, L. Q., Iacoboni, M., Lange, C., & Keenan, J. P. (2007). The self and social cognition: The role of cortical midline structures and mirror neurons. *Trends in Cognitive Sciences*, *11*(4), 153–157. doi:10.1016/j.tics.2007.01.001
- Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic stimulation of extrastriate body area impairs visual processing of nonfacial body parts. *Current Biology*, *14*(23), 2130–2134. doi:10.1016/j.cub.2004.11.031
- Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*(3), 533–551. doi:10.1007/s00221-008-1562-y
- Van Boven, R. W., & Johnson, K. O. (1994). The limit of tactile spatial resolution in humans: Grating orientation discrimination at the lip, tongue, and finger. *Neurology*, *44*(12), 2361–2361. doi:10.1212/WNL.44.12.2361
- Verosky, S. C., & Todorov, A. (2010). Differential neural responses to faces physically similar to the self as a function of their valence. *NeuroImage*, *49*(2), 1690–1698. doi:10.1016/j.neuroimage.2009.10.017
- Vocks, S., Busch, M., Grönemeyer, D., Schulte, D., Herpertz, S., & Suchan, B. (2010). Differential neuronal responses to the self and others in the extrastriate body area and the fusiform body area. *Cognitive, Affective, & Behavioral Neuroscience*, *10*(3), 422–429. doi:10.3758/CABN.10.3.422
- Wang, J., Fan, L., Zhang, Y., Liu, Y., Jiang, D., Zhang, Y., ... Jiang, T. (2012). Tractography-based parcellation of the human left inferior parietal lobule. *NeuroImage*, *63*(2), 641–652. doi:10.1016/j.neuroimage.2012.07.045

- Wan, M., Bolger, N., & Champagne, F. A. (2012). Human perception of fear in dogs varies according to experience with dogs. *PLoS ONE*, *7*(12), e51775.
doi:10.1371/journal.pone.0051775
- Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation: Report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5–7, 1996. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *108*(1), 1–16.
doi:10.1016/S0168-5597(97)00096-8
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *The Journal of Neuroscience*, *18*(1), 411–418.
- Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion*, *1*(1), 70–83. doi:10.1037/1528-3542.1.1.70
- Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *The Journal of Neuroscience*, *24*(12), 2898–2904.
doi:10.1523/JNEUROSCI.4977-03.2004
- Willis, W. D., Kenshalo, D. R., Jr., & Leonard, R. B. (1979). The cells of origin of the primate spinothalamic tract. *The Journal of Comparative Neurology*, *188*(4), 543–573.
doi:10.1002/cne.901880404
- Winston, J. S., Henson, R. N. A., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology*, *92*(3), 1830–1839. doi:10.1152/jn.00155.2004

- 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.
doi:10.1038/2245
- Wrigley, P. J., Press, S. R., Gustin, S. M., Macefield, V. G., Gandevia, S. C., Cousins, M. J., ... Siddall, P. J. (2009). Neuropathic pain and primary somatosensory cortex reorganization following spinal cord injury. *Pain*, *141*(1–2), 52–59. doi:10.1016/j.pain.2008.10.007
- Yamamura, H., Iwata, K., Tsuboi, Y., Toda, K., Kitajima, K., Shimizu, N., ... Sumino, R. (1996). Morphological and electrophysiological properties of ACCx nociceptive neurons in rats. *Brain Research*, *735*(1), 83–92. doi:10.1016/0006-8993(96)00561-6
- Young, A. W., Aggleton, J. P., Hellawell, D. J., Johnson, M., Broks, P., & Hanley, J. R. (1995). Face processing impairments after amygdalotomy. *Brain*, *118*(1), 15–24.
doi:10.1093/brain/118.1.15
- Young, A. W., Hellawell, D. J., Van de Wal, C., & Johnson, M. (1996). Facial expression processing after amygdalotomy. *Neuropsychologia*, *34*(1), 31–39. doi:10.1016/0028-3932(95)00062-3
- Zhang, Z. G., Hu, L., Hung, Y. S., Mouraux, A., & Iannetti, G. D. (2012). Gamma-band oscillations in the primary somatosensory cortex—A direct and obligatory correlate of subjective pain intensity. *The Journal of Neuroscience*, *32*(22), 7429–7438.
doi:10.1523/JNEUROSCI.5877-11.2012
- Zhu, Q., Nelissen, K., Van den Stock, J., De Winter, F.-L., Pauwels, K., de Gelder, B., ... Vandenbulcke, M. (2013). Dissimilar processing of emotional facial expressions in human and monkey temporal cortex. *NeuroImage*, *66*, 402–411.
doi:10.1016/j.neuroimage.2012.10.083
- Zilles, K. (1990). Cortex. In G. Paxinos (Ed.), *The Human Nervous System* (pp. 757–802). San Diego, CA: Academic Press.