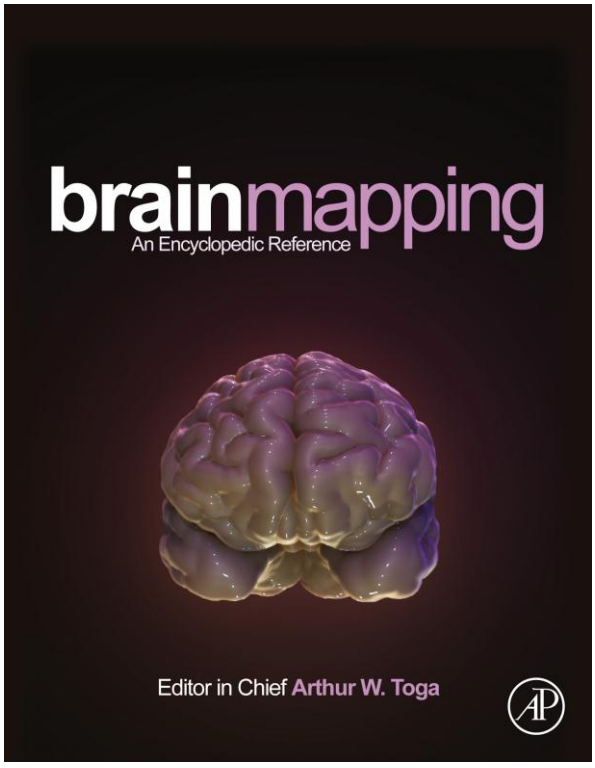
Provided for non-commercial research and educational use.
Not for reproduction, distribution or commercial use.

This article was originally published in Brain Mapping: An Encyclopedic Reference, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

http://www.elsevier.com/locate/permissionusematerial

de Gelder B., and de Borst A.W. (2015) Body Perception. In: Arthur W. Toga, editor. *Brain Mapping: An Encyclopedic Reference*, vol. 3, pp. 107-114. Academic Press: Elsevier.

Author's personal copy

Body Perception

B de Gelder, Psychology and Neuroscience, Maastricht Brain Imaging Centre, Maastricht University, Maastricht, The Netherlands
AW de Borst, Psychology and Neuroscience, Cognitive Neuroscience, Maastricht University, Maastricht, The Netherlands

© 2015 Elsevier Inc. All rights reserved.

Why Bodies?

Given the prominence of bodies in the socioemotional environment, it is rather puzzling that in the last decades, with the meteoric rise of research publications on social and affective neuroscience, body perception has received little attention. While the amount of neuroimaging studies on face perception has increased dramatically, the studies on body perception still lag behind significantly. It is seemingly presumed that faces are a more universal and consistent carrier of (emotional) information than bodies. However, recent behavioral and neuroimaging research shows that recognition performance of bodily expressions is fairly similar to that of facial expressions (Atkinson, Dittrich, Gemmell, & Young, 2004; de Meijer, 1989; Dittrich, Troscianko, Lea, & Morgan, 1996; Hadjikhani & de Gelder, 2003; Wallbott, 1998) and that bodies activate an extensive network of brain regions, including regions that are responsive to faces (Downing, Jiang, Shuman, & Kanwisher, 2001; Schwarzlose, Baker, & Kanwisher, 2005; Spiridon, Fischl, & Kanwisher, 2006; van de Riet, Grèzes, & de Gelder, 2009). Bodies carry information on the actions and, possibly, intentions of others (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Gallese, Fadiga, & Rizzolatti, 1998) and are highly relevant for transferring social cues (de Gelder, 2006; Keysers, Kaas, & Gazzola, 2010). With the recent shift in neurosciences towards more ecologically valid stimuli (Bartels & Zeki, 2004; Hasson, Nir, Levy, Fuhrmann, & Malach, 2004), the interest in the body as a natural and socially significant stimulus has risen. Especially, the investigation of bodily expressions – from either an emotion or action perspective – provides more information about the perception of bodies under natural conditions. Hence, we will discuss, for different research methods, evidence from both neutral body perception and perception of bodily expressions to form a complete picture of how bodies are perceived. First, we present a short overview of behavioral studies on body perception that form the basis for subsequent neuroimaging studies. We then look in more detail at the brain regions involved in body perception and the underlying neural dynamics.

Behavioral Studies on Body Perception

Body Processing

At the behavioral level, there is clear evidence that both faces and bodies are processed as a configuration rather than as an assemblage of separate features. This is indicated by the ability to perceive a complex image as an integrated whole. A classical way of measuring people's ability to do so is to compare recognition performance for the same stimulus shown in its canonical orientation or upside down (Yin, 1969). The resulting difference in performance has been dubbed the 'inversion effect,' referring to the loss of performance when upside-down stimuli have to be recognized, compared with upright stimuli. Contrary to what is often assumed, this is not specific to faces. A similar loss of performance is also observed for other stimuli, for example, landscapes. Recent findings show that recognition of both faces and bodies presented upside down is relatively more impaired than recognition of other objects presented upside down, when recognition rates of each category are compared with recognition rates of the inverted counterpart (Reed, Stone, Bozova, & Tanaka, 2003). This suggests that bodies, like faces, are processed configurally.

Body Affect Recognition

In addition to investigating how bodies are perceptually processed, another line of research explored how bodies convey information. Ekman first investigated bodies as affect communicators in 1965. While he concluded that faces and bodies communicate affect in a different manner, more recent behavioral research shows that recognition performance of expressions is quite similar for face and body stimuli. This applies to studies with static as well as dynamic whole-body stimuli. The available studies have indeed found a high degree of agreement among observers (Atkinson et al., 2004; de Meijer, 1989; Dittrich et al., 1996; Hadjikhani & de Gelder, 2003; Wallbott, 1998). In order to further investigate body expressions with neuroimaging techniques, a stimulus set of still whole-body expressions has been developed: the bodily expressive action stimulus test (BEAST; de Gelder & Van den Stock, 2011). All displayed bodily emotions (happy, sad, anger, and fear) in this stimulus set were correctly categorized in at least 85% of the cases. A similarly high consensus is found for video clips depicting emotions or instrumental actions performed with a specific emotion, for example, hearing the doorbell and opening the door in an angry way (Grèzes, Pichon, & de Gelder, 2007). Recognition rates were around 10% higher for dynamic images than for their still counterparts. Naturally, these rates increased another 10% when the face was not blanked out. However, higher recognition rates for the addition of dynamic and facial information may simply be related to the amount of information in the stimulus. Obviously, there is more information in a video clip than in a still image, and showing the full face rather than blurring it adds more information again. In short, it appears that consensus for recognition of bodily expressions among viewers is as substantial as the consensus for recognition of facial expressions when tested with comparable stimuli under similar viewing conditions.

Interaction between Faces and Bodies

In the real world, bodies and faces are almost never perceived in isolation, but rather as an integrated whole. Two behavioral studies investigated how recognition of facial expressions is influenced by the accompanying whole-body expressions. Meeren, van Heijnsbergen, and de Gelder (2005) presented

Author's personal copy

participants with congruent (fearful face on fearful body and angry face on angry body) or incongruent (fearful face on angry body and angry face on fearful body) compound stimuli, while they had to categorize the facial expression and ignore the bodily expression. The results showed that recognition of the facial expression was biased towards the emotion expressed by the body language, as reflected by both the accuracy and reaction time data. In a follow-up study, facial expressions that were morphed on a continuum between happy and fearful were then combined with a happy or fearful whole-body expression (van den Stock, Righart, & de Gelder, 2007). Again, the ratings of the facial expressions were influenced towards the emotion expressed by the body, and this influence was highest for facial expressions that were most ambiguous (expressions that occupied an intermediate position on the morph continuum).

In conclusion, behavioral research has shown that bodies are perceived as an integrated whole and its expressions are well recognized. When face and the body expressions are shown simultaneously, they exert influence on each other even if the task demands recognition of only one.

Neural Basis of Body Perception

Neuroscience research has further investigated the processing of bodies by looking at its underlying neural mechanisms. Single-cell recordings and functional magnetic resonance imaging (fMRI) studies have revealed brain areas that are specifically responsive to bodies. Also, bodily expression of emotion and action has been shown to activate unique brain networks that help us understand social signals of others.

Evidence from Single-Cell Recordings

Neural Representation of Neutral Bodies

Neurophysiological studies of body processing started with single-cell recording studies in the monkey. In the late 1960s, Gross, Bender, and Rocha-Miranda (1969) and Gross, Rocha-Miranda, and Bender (1972) found neurons in the inferior temporal cortex (IT) that selectively fired to silhouettes of monkey hands. This result was later confirmed for drawings of human hands and faces (Desimone, Albright, Gross, & Bruce, 1984). Evidence for body shape specificity in monkeys was found recently by Kiani, Esteky, Mirpour, and Tanaka (2007) who recorded from a large population of single cells in IT. The response pattern of the cell population as a whole was far more category-selective than that of single cells, implying that not only cell responses to the preferred category but also responses to the suboptimal categories carry important information. The population responses formed category clusters that resembled our intuitive object categories, with a first main division between animals and inanimate objects. The animal-characteristic responses could be divided into face- and body-related responses, and these could be further subdivided on the basis of certain animal classes, with the body population code forming three distinct clusters, that is, for human bodies, four-limbed animals and birds and lower animals. Liu et al. (2013) proposed that objects in IT are represented both modular and distributed in a recent study in which monkeys were presented with a wide range of objects. They showed categorical structure in IT, distinguishing animate from inanimate objects, with faces as a substructure of the animate objects. No such structure was found in the V4, amygdala, and prefrontal cortex. The posterior face-selective patch in IT showed smaller dissimilarity for within-face and within-body category compared with between-face inanimate categories, while this was only true for faces in the anterior face-selective patch.

Additionally, neurons responding to various types of static body images such as body orientations, body postures that implied motion, and body movements were discovered in the STS (Barraclough, Xiao, Oram, & Perrett, 2006; Jellema & Perrett, 2003a, 2003b; Oram & Perrett, 1996; Perrett et al., 1985; Wachsmuth, Oram, & Perrett, 1994). These cells in the STS seem to be responsive to not only moving stimuli but also static images that imply motion, suggesting a role in social perception. This role of the STS and specifically posterior STS in body perception has since been confirmed in studies using social signal stimuli (e.g., Allison, Puce, & McCarthy, 2000; de Gelder & Partan, 2009; Peelen, Atkinson, & Vuilleumier, 2010).

Body action

While the perception of bodies is the main focus in this article, we cannot omit influential work that has been performed on the perception of motor action, since body representation and action are so closely linked. In 1996, a group of researcher discovered 'mirror' neurons in the parietal and premotor cortices of the macaque monkey brain. These neurons were seen to discharge not only when the monkey performed an action but also when observing an experimenter or another monkey performed the same action (di Pellegrino et al., 1992; Fogassi et al., 1998). These results support the notion that when one observes the action of another, the motor program of the observed action is activated in the observer's brain. The same seems to hold for bimodal visuotactile neurons in the monkey parietal cortex when observing visual or tactile stimuli placed on others' body parts (Ishizu, Amemiya, Yumoto, & Kojima, 2010). It seems to be only a small step then to go on suggesting that observers use their own motor system to perceive the action of others. Indeed, current evidence suggests that the extent and level of activity within those regions are constrained by the observer's motor abilities, in both monkeys (Rochat et al., 2010; Umiltà et al., 2008) and humans (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006).

While these single-cell recording studies provide information on the specificity of activation in neuronal populations to different types of body-related stimuli, the extent to which these region-specific mechanisms function similarly in humans can only be tested noninvasively using positron emission tomography or fMRI studies.

Evidence from fMRI Studies

Neural representation of neutral bodies

Since a large proportion of neuroscience research in the last decade has focused on face perception, it has formed a natural starting point for the study of body perception. Upon its first

Author's personal copy

discovery, the FFA was seen as a main hub for processing faces (Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). Together with other category-selective areas in the OTC, it was thought to form a network of brain regions that processed specific types of objects. However, evidence emerged that the FFA, rather than being a face-specific region, might reflect experience-based specialization (Gauthier & Tarr, 1997). In a similar fashion, the body perception literature has initially focused on finding *the* 'body region' like the FFA. Functional MRI in monkeys revealed specialized patches for faces and bodies within the object-selective cortex (Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). These results can be linked to the human object-selective cortex, since evidence has been provided that there are similarities in object representation in the monkey and the human brain (Kriegeskorte et al., 2008). Additionally, the macaque and the human face show close anatomical correspondence, as well as the face and body processing systems (Pinsk et al., 2009; Tsao, Moeller, & Freiwald, 2008).

In humans, fMRI investigations into the brain basis of body perception have shown that bodies activate (to smaller or larger extend) the same brain areas that were hitherto associated with the perception of faces (for reviews, see de Gelder, 2006; Peelen & Downing, 2007). It has been suggested that the mid-fusiform gyrus (FG) might contain multiple closely spaced category-selective regions that are partially overlapping (Peelen & Downing, 2005). One such region in the mid-FG, the fusiform body area (FBA), partially overlaps with the FFA but was found to respond to whole bodies (Hadjikhani & de Gelder, 2003; Peelen & Downing, 2005; Schwarzlose et al., 2005; Spiridon et al., 2006). This has also been confirmed for perceiving bodily expressions (van de Riet et al., 2009). Moreover, earlier research has revealed a distinct area in the occipitotemporal cortex (OTC), the so-called extrastriate body area (EBA), that activates more to neutral bodies than to other object categories, including faces (Downing et al., 2001). These category-specific results have mostly been studied using neutral bodies. When viewing whole-body expressions, activity in a wide network of brain areas is elicited, including, but not confined to, other areas previously associated with perception of facial expressions, like the STS. Other brain regions involved in body perception include the superior occipital gyrus (SOG) and the parieto-occipital sulcus (POS). Functional analogies have been proposed between the relatively early face feature-sensitive OFA and the body part-sensitive EBA on the one hand and between the later face-sensitive FFA and body-sensitive FBA on the other hand (Taylor, Wiggett, & Downing, 2007). This was hypothesized on the basis of their anatomical proximity as well as their relative sensitivity to facial features and body parts. Analogous to face processing, Taylor et al. (2007) suggested that the EBA might process the separate body parts and that this information is subsequently integrated as a whole in the FBA.

However, next to the object representation model that presumes category-specific modules in OTC, there is also growing evidence for another model in which visual features are represented in a distributed manner in OTC and objects are expressed as a combination of these features (Haxby et al., 2001; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). Recently, Weiner and Grill-Spector (2011) investigated EBA using convergent evidence from anatomical landmarks, visual field maps, and functional stimulus comparisons. They conclude that EBA must not be considered a single area but that there is a sparsely distributed network of body representations. Within this network, at least three different separate limb-selective activations can be distinguished, which might be even further parcellated with newer techniques in the future. Importantly, the authors speculate that the three limb-selective activations, which are organized in a crescent surrounding hMT+, may be a direct reflection of underlying anatomical differences between MT+ and the surrounding cortex. It is not yet well understood what the specific functions are of these anatomically defined areas.

Bodies versus faces

Only a few fMRI investigations in humans have made a direct comparison between faces and bodies (emotional body parts: Grosbras & Paus, 2006; neutral: Thompson, Hardee, Panayiotou, Crewther, & Puce, 2007). Since bodies and faces have very different visual features, direct comparison of these categories should be interpreted with care. van de Riet et al. (2009) showed that when comparing the hemodynamic responses of faces versus bodies, the perception of bodies triggered a broad network of brain areas, including areas previously associated with perception of faces – including the FG, the STS, and the middle occipital gyrus. Additionally, the SOG, the POS, and the intraparietal sulcus responded more to bodies than to faces. Areas more responsive to faces than bodies were restricted to the calcarine sulcus, cerebellum, superior frontal gyrus, and anterior cingulate gyrus. Other studies typically focus on the FG and compare areas that respond more to bodies than to objects with areas that respond more to faces than to objects, rather than a direct comparison between faces and bodies (Peelen & Downing, 2005; Schwarzlose et al., 2005; Spiridon et al., 2006). Using this indirect comparison approach, a previous study by Schwarzlose et al. (2005) found an effect of scanning resolution on the selectivity for either faces or bodies in the FG, with a positive correlation between selectivity and resolution. Their results showed a higher selectivity for faces in the FG, which corroborates the results of a subsequent study of the same lab (Spiridon et al., 2006) but shows the inverse pattern compared to van de Riet et al. (2009). This may be related to methodological issues, such as scanning parameters, the contrasts applied in the data analysis, and the different object categories that were presented.

Additionally, other issues hamper a direct comparison of faces and bodies. First, the face is only a part of an object (person), whereas a body (even with the facial area blurred) constitutes a complete object. This may play a role not only in the comparison of faces with objects but also in indirect comparisons: faces versus objects compared with bodies versus objects. Second, perception of faces allows a detailed and fine-grained analysis of the complex musculature of the face, whereas bodies are generally covered with clothing, which may conceal important information about muscle tension, especially when dealing with emotional expressions. Also, the presence of clothing implies perception of man-made objects, whereas faces are typically presented in isolation.

Author's personal copy

Body action

There are more dimensions of information conveyed by bodies than their category identity. An important aspect is the action shown by the body. Using repetitive transcranial magnetic stimulation (rTMS) in healthy individuals, Urgesi, Calvo-Merino, Haggard, and Aglioti (2007) showed that interference with the EBA impairs the discrimination of bodily forms and interference with the ventral premotor cortex impairs the discrimination of bodily actions. This finding was later confirmed by a lesion study investigating body perception in a prosopagnosic patient (Moro et al., 2008). This double dissociation suggests that whereas the EBA mainly processes body identity, the premotor cortex is crucial for visual discriminations of actions (Moro et al., 2008; see also Taylor et al., 2007; Urgesi et al., 2007). Urgesi et al. (2007) suggested that bodies are processed in two pathways: the frontoparietal mirror network contributes to configural processing of bodies, while the body shapes are processed in the EBA. This is in line with other models of body processing (Taylor et al., 2007) and fMRI evidence for the processing of body action within the mirror neuron framework (Pobric & Hamilton, 2006; Rizzolatti & Craighero, 2004). Vangeneugden, Peelen, Tadin, and Battelli (2014) confirmed the role of the EBA in body form discrimination using TMS and in addition showed that the posterior STS also seems to play a role in body motion discrimination. Since the STS receives input from both dorsal and ventral streams, it is a likely candidate for form-motion integration (Mather, Pavan, Bellacosa Marotti, Campana, & Casco, 2013). Moreover, the posterior STS seems to play an important role in not only social perception, including biological motion, but also other social signals such as emotions, as discussed in the succeeding text (Lahnakoski et al., 2012). The close link between action and bodies is further confirmed by Bracci and Peelen (2013), who showed that body effectors and object effectors share common representations in the LOTC and parietal cortex. These fMRI results suggest that part of the hierarchical structure incorporates body–object relations.

Emotional body perception

Although part of social signaling is done through action representations, another natural part of social interaction is emotion conveyance. Similar to studies that reported emotional modulation of face-specific areas, like the FFA and OFA (e.g., Breiter et al., 1996; van de Riet et al., 2009; Vuilleumier, Armony, Driver, & Dolan, 2001), other studies have explored the effects of the presence of emotional information on activation levels of body areas in the brain. The first study addressing this issue focused on the FG and amygdala (AMG) and found an increased activation for fearful bodies compared with instrumental bodies in both areas (Hadjikhani & de Gelder, 2003). This result was very similar to the most frequently observed result for faces and is consistent with an AMG–FG connection. In a follow-up experiment, whole brain activation to fearful, happy, and neutral body expressions was compared (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004). A major finding of that study was the involvement of motor areas in the perception of emotional body expressions. Similar results were obtained in a study that directly compared neutral and emotional faces and bodies (van de Riet et al., 2009). Emotional bodies activated cortical and subcortical motor-related structures, such as the inferior frontal gyrus, caudate nucleus, and putamen. These motor areas were not active for emotional faces. Whether EBA is also modulated by emotion remains uncertain. Although no difference was observed between neutral and emotional bodies using static body images (Lamm & Decety, 2008; van de Riet et al., 2009), several findings suggest that the EBA is doing much more than merely processing body parts. First, rTMS over EBA reduced aesthetic sensitivity for body stimuli relative to rTMS over vPMC, and the absence of such a difference for nonbody stimuli suggests that EBA is involved in the aesthetic evaluation of body stimuli (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010). Second, emotion modulation in both EBA and FBA has been observed in studies that use dynamic body expressions (Grèzes et al., 2007; Peelen, Atkinson, Andersson, & Vuilleumier, 2007; Pichon, de Gelder, & Grèzes, 2008). Third, EBA also shows increased activation level when observers are watching a fear-inspiring visual scene, like a damaged car or a house on fire that does not show any people in it (Sinke, Van den Stock, Goebel, & de Gelder, 2012).

The (posterior) STS also plays a role in emotional body perception and the perception of other social signals. Peelen et al. (2010) found modality-independent multivoxel patterns for faces, bodies, and houses that showed emotion-specific responses. Similarly, using natural stimuli, Lahnakoski et al. (2012) uncovered responses to a.o. emotion and bodies in the posterior STS. Also in monkeys, socially relevant bodily emotions are processed in the STS (de Gelder & Partan, 2009).

The Temporal Dynamics of Body Perception

Despite the growing number of fMRI studies on body perception, there are many questions on its underlying neural mechanisms that remain unanswered. For example, to understand whether body images are processed first part by part in the EBA and then later – as a whole integrated stimulus – in FG, one needs to understand the time course of activation of the regions involved. In general, it is difficult to form a proper functional neural model without a better understanding of the time course of activity in the cortical areas. Such information on timing in human brain processes should come from electrophysiological studies, while hemodynamic responses do not provide direct information about fast-changing temporal dynamics of perception. While the neurophysiology of face processing in humans has been extensively studied with the use of electroencephalography (EEG) and magnetoencephalography (MEG), information on the timing of activation during body perception is still very scarce. Here, we will review evidence on the temporal signature of body perception though EEG and MEG.

Evidence from EEG

By far, the most useful information on the time course of body-selective processing in the human brain has been obtained from noninvasive electrophysiological recordings. Overall, a strong suggestion from the available studies is that the event-related potentials (ERPs) for face and body perception show

Author's personal copy

several similarities (Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Righart & de Gelder, 2007; Stekelenburg & de Gelder, 2004; Thierry et al., 2006). For example, ERPs for faces as well as for bodies show a P1 and a prominent N1 component with similar scalp topography (Stekelenburg & de Gelder, 2004). The N1, best known as the 'N170 for face perception,' a negative deflection at occipitotemporal electrodes peaking between 140 and 220 ms poststimulus onset, presumably reflects the structural encoding of the visual stimulus (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000b). The mean peak latency of the N1 component for body processing has been found to range between 154 and 228 ms after stimulus onset and is sometimes referred to as the N190 (Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Minnebusch & Daum, 2009; Righart & de Gelder, 2005; Stekelenburg & de Gelder, 2004; Thierry et al., 2006; van Heijnsbergen, Meeren, Grèzes, & de Gelder, 2007). These initial findings seem to suggest that the structural processing of faces and bodies takes place in approximately the same time window.

When looking at these time courses in more detail and comparing them directly between faces and bodies, the peak latency of the N170 for whole human bodies that include heads but with the face masked was found to be faster than that for faces (Meeren et al., 2005; Righart & de Gelder, 2007; Stekelenburg & de Gelder, 2004). However, when headless bodies are presented, the N170 response seems delayed and becomes slower than that for faces (Gliga & Dehaene-Lambertz, 2005; Thierry et al., 2006). When analyzed at a higher spatial resolution, the body and face N170 showed a different spatial pattern, in both their potential distribution on the scalp (Gliga & Dehaene-Lambertz, 2005) and their corresponding source localizations in the brain (Thierry et al., 2006). However, as pointed out earlier, it is potentially misleading to compare directly within a single design what the temporal signature is of stimulus categories with very different physical properties. The ERP signal can be sensitive to such physical stimulus differences, and direct comparisons between faces and bodies may be misleading. For this reason, some studies adopted the approach to use the inverted presentation of each stimulus category as the marker for comparison. Adopting that criterion, the inversion effect is of the same magnitude for faces and bodies (Stekelenburg & de Gelder, 2004). A study by Bauser and Suchan (2013) confirmed earlier findings that inverted faces and bodies elicited stronger amplitudes of N170 and delayed behavioral responses compared with upright faces and bodies. Moreover, they found that stimulus distortion disrupts the body, but not the face inversion effect, hinting at different processing pathways for both types of stimuli.

One can imagine many more ways of measuring specific aspects of bodies and body expressions and how they influence the P1, the N170, and the VPP. A glance at the ERP–face literature illustrates the wide range of possibilities that have been attempted in the domain of faces. Notably, a recent study continued exploration of the N170 as a marker of a.o. body-sensitive processing (Hietanen & Nummenmaa, 2011). They explored the role of nude over clothed bodies by comparing responses to nude bodies, bodies wearing swimsuits, clothed bodies, faces, and cars. All types of human stimuli evoked greater N170 responses than the cars. The N170 amplitude was larger to opposite and same-sex nude versus clothed bodies. Moreover, the N170 amplitude increased linearly as the amount of clothing decreased from full clothing via swimsuits to nude bodies. Strikingly, the N170 response to nude bodies was even greater than that to faces, and the N170 amplitude to bodies was independent of whether the face of the bodies was visible or not.

Evidence from MEG

The time window within which the N170 is measured offers just one view on the underlying processes of body perception. The information it provides does not directly tell us much about the neural basis of these processes. For example, there may be different underlying neural generators for face and body perception in what looks like one and the same N170 time window. Another noninvasive technique that may be better suited to provide information on the time course of body perception and its underlying sources is MEG. Since gathering and analyzing MEG data are more complex than EEG, and MEG machines are less available than fMRI scanners, little MEG studies have been performed on body perception thus far. However, source analyses for MEG are much more precise than EEG and can provide valuable information to link temporal and spatial information from EEG and fMRI studies, respectively. To date, there is only one EEG study on the body N170 that employed source localization (Thierry et al., 2006), showing largely overlapping source maps for bodies and faces in the right posterior extrastriate cortex. However, it remains difficult to interpret these localization results, since they lack spatial accuracy and specificity. As the authors state, the contribution of neural generators to the N170 and N190 still has to be explored further.

A study by Ishizu et al. (2010) provides clarification on the sources of the body N170. In this MEG study, neural responses to faces, bodies, and objects were compared. The results revealed a P100 component that was equally responsive to all categories and an N170 for faces and N190 for bodies. They localized the N190 to body perception in the right-dominated middle temporal gyrus (approximately EBA). The N170s to face and object perception were localized in clearly separate regions in, respectively, the posterior inferior IT and posterior middle temporal gyrus. These results were further confirmed by another study that compared evoked responses to faces, bodies, and control stimuli and modeled its underlying sources (Meeren, de Gelder, Ahlfors, Hämäläinen, & Hadjikhani, 2013). Differences were found in face and body processing networks. Activity to face images peaked around 140 ms poststimulus and recruited a widespread distributed network of cortical areas involving early activation of the LOC, LOTC, and VTC (including the functional areas of the OFA and the FFA), corresponding to the time window of the visual analysis and structural encoding of the stimulus (Eimer, 2000a,2000b). In contrast, around 150 ms bodies activate a much more restricted area in the LOTC (including the functional area of the EBA), suggesting that the main area for the visual analysis of bodies is the EBA and not the FBA. Extensive body-selective cortical activation occurred at later latencies in dorsal, frontal, and temporal regions, with the OFC showing significant body-selective responses after 200 ms after stimulus

Author's personal copy

onset and the VTC and LTC after 500 ms latency. These MEG results suggest that the hemodynamic activation of the FBA by bodies found in fMRI studies (Hadjikhani & de Gelder, 2003; Peelen & Downing, 2005; Schwarzlose et al., 2005; Spiridon et al., 2006; van de Riet et al., 2009) may in fact reflect later stages of visual recognition and not the visual analysis per se.

Information on the onset and localization of inversion effects of faces and bodies was provided by an MEG study of Meeren, Hadjikhani, Ahlfors, Hamalainen, and de Gelder (2008). Both faces and bodies showed early inversion effects between 70 and 100 ms post stimulus, with larger responses for the inverted images. Interestingly, the cortical distribution of this early inversion effect was highly category-specific. For faces, it was found in well-known face-selective regions (e.g., the right inferior occipital gyrus and mid-FG), whereas for bodies, it was found in the medial parietal areas. Hence, whereas face inversion influences early activity in face-selective regions in the ventral stream, body inversion makes a difference for activity in dorsal stream areas. This seems to suggest that there are different early cortical pathways for the perception of face and body images. Additionally, there may be different time courses of activation in the common or partly overlapping neural substrate of faces and bodies in the FG.

In conclusion, MEG has allowed us to shed a first light on the time courses of cortical areas involved in the visual perception of whole human bodies and their emotional expressions. Whereas the MEG findings provide evidence for a prominent role of the EBA in early body perception, so far, there is no evidence for an involvement of the FG/FBA during the visual perception stage. Instead, the results suggest a different possibly postperceptual modulatory role for the FBA/FG. Future electrophysiological studies are needed with more diverse stimulus material and task demands to further investigate the cognitive response profile of the FBA. Direct cortical recordings from the temporal lobe in epileptic patients would be invaluable to further elucidate the time courses of the FG and lateral temporal lobe in body processing, while ingenious fMRI designs could further dissect the functional role of the FG in body processing. What has become clear is that face processing and body processing have their own unique activation pattern with qualitative differences in both the cortical and subcortical networks involved and their time evolution.

Time Course of Developing Body Perception Skills

In view of the classic claim that our emotional expressions have a solid evolutionary history, one expects that evidence for their perception and production can already be seen in the early stages of infancy. Many methods used to study normal adult body perception are obviously not ideal for developmental researchers. However, EEG measurements are a valuable method for studying neural dynamics in infants. These methods have been used frequently when studying early language perception or visual processes, like the perception of causality. In the domain of social signal perception, the investigation of face perception occupies the first place, while studies on body recognition in infants are very rare. Gliga and Dehaene-Lambertz (2007) showed that distorted body perception compared with intact body perception has an effect on the P400 in 3-month-old infants. These results suggest that configural body processing already takes place in 3-month-old infants, although at a different time point compared to adults (N1). A preference for happy rather than neutral whole-body video clips is shown in 6.5-year-old infants. This preference disappeared when the images were shown upside down (Zieber, Kangas, Hock, & Bhatt, 2014). When viewing bodily actions, 14-month-old infants show mu synchronization over the sensorimotor cortex with specificity for hand versus foot actions (Saby, Meltzoff, & Marshall, 2013). As is often the case, the fact that time is needed for evidence of a skill to show does not directly prove that the skill needs learning or exposure. These and similar questions about nature versus nurture of basic social skills are difficult to answer. But on the face of it, and measured with techniques similar to those used in normal adults, there does indeed seem to be a change over time. Neither face nor voice or body expression recognition manifests itself before some months. Whether or not the behavioral manifestation of the skill is in fact dependent on or waiting for neural maturation remains an open question.

Future Directions

Research on the perception and experience of bodily expressions can be taken in a number of different directions. First of all, more electrophysiological work is needed to clarify the role of several prominent brain regions in body perception. Second, neuroimaging work could elaborate into the domain of natural neuroscience by replacing still picture with video clips, placing body expressions in natural and social contexts (Van den Stock, Vandenbulcke, Sinke, & de Gelder, 2014), or, even more innovatively, studying actual interactions between two or more people. Moreover, studying integration between bodily expressions and auditory information, such as voices or music, can lead to a more comprehensive view on natural body perception.

See also: **INTRODUCTION TO CLINICAL BRAIN MAPPING**: Limbic to Motor Interactions during Social Perception; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE**: Action Perception and the Decoding of Complex Behavior; Emotion Perception and Elicitation; The Neural Correlates of Social Cognition and Social Interaction; The Use of Brain Imaging to Investigate the Human Mirror Neuron System; **INTRODUCTION TO SYSTEMS**: Action Understanding; Face Perception; Neural Codes for Shape Perception.

References

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*(7), 267–278.

Atkinson, A. P., Dittrich, W. H., Gemmell, A. J., & Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception*, *33*, 717–746. http://dx.doi.org/10.1068/p5096.

Barraclough, N. E., Xiao, D., Oram, M. W., & Perrett, D. I. (2006). The sensitivity of primate STS neurons to walking sequences and to the degree of articulation in static images. *Progress in Brain Research*, *154*, 135–148.

Bartels, A., & Zeki, S. (2004). Functional brain mapping during free viewing of natural scenes. *Human Brain Mapping*, *21*, 75–85.

Bauser, D. S., & Suchan, B. (2013). Behavioral and electrophysiological correlates of intact and scrambled body perception. *Clinical Neurophysiology*, *124*(4), 686–696.

Author's personal copy

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of Face Perception in Humans. *Journal of Cognitive Neuroscience*, *8*(6), 551–565.

Bracci, S., & Peelen, M. V. (2013). Body and object effectors: the organization of object representations in high-level visual cortex reflects body-object interactions. *Journal of Neuroscience*, *33*(46), 18247–18258.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., et al. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, *17*(5), 875–887.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243–1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*(19), 1905–1910.

Calvo-Merino, B., Urgesi, C., Orgs, G., Aglioti, S. M., & Haggard, P. (2010). Extrastriate body area underlies aesthetic evaluation of body stimuli. *Experimental Brain Research*, *204*(3), 447–456.

Cross, E. S., Hamilton, A. F., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, *31*(3), 1257.

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

de Gelder, B., & Partan, S. (2009). The neural basis of perceiving emotional bodily expressions in monkeys. *Neuroreport*, *20*(7), 642–646.

de Gelder, B., Snyder, J., Greve, D., Gerard, G., & Hadjikhani, N. (2004). Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(47), 16701–16706.

de Gelder, B., & Van den Stock, J. (2011). The bodily expressive action stimulus test (BEAST). Construction and validation of a stimulus basis for measuring perception of whole body expression of emotions. *Frontiers in Psychology*, *2*, 181.

de Meijer, M. (1989). The contribution of general features of body movement to the attribution of emotions. *Journal of Nonverbal Behavior*, *13*(4), 247–268. http://dx.doi.org/10.1007/BF00990296.

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *The Journal of Neuroscience*, *4*(8), 2051–2062.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*(1), 176–180.

Dittrich, W. H., Troscianko, T., Lea, S. E., & Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception*, *25*(6), 727–738.

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. http://dx.doi.org/10.1126/science.1063414.

Eimer, M. (2000a). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, *111*(4), 694–705.

Eimer, M. (2000b). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, *11*(10), 2319–2324.

Fogassi, L., Gallese, V., Fadiga, L., & Rizzolatti, G. (1998). Neurons responding to the sight of goal-directed hand/arm movements in the parietal area PF (7b) of the macaque monkey. *Society of Neuroscience Abstracts*, *24*, 257.255.

Gauthier, I., & Tarr, M. J. (1997). Becoming a "Greeble" expert: Exploring mechanisms for face recognition. *Vision Research*, *37*(12), 1673–1682.

Gliga, T., & Dehaene-Lambertz, G. (2005). Structural encoding of body and face in human infants and adults. *Journal of Cognitive Neuroscience*, *17*, 1328–1340.

Gliga, T., & Dehaene-Lambertz, G. (2007). Development of a view-invariant representation of the human head. *Cognition*, *102*(2), 261–288.

Grèzes, J., Pichon, S., & de Gelder, B. (2007). Perceiving fear in dynamic body expressions. *NeuroImage*, *35*(2), 959–967. http://dx.doi.org/10.1016/j.neuroimage.2006.11.030.

Grosbras, M.-H., & Paus, T. (2006). Brain networks involved in viewing angry hands or faces. *Cerebral Cortex*, *16*(8), 1087–1096.

Gross, C. G., Bender, D. B., & Rocha-Miranda, C. E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, *166*(910), 1303–1306.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, *35*(1), 96–111.

Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology*, *13*(24), 2201–2205.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *Science*, *303*, 1634–1640.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*(5539), 2425–2430.

Hietanen, J. K., & Nummenmaa, L. (2011). The naked truth: The face and body sensitive N170 response is enhanced for nude bodies. *PLoS One*, *6*(11), e24408.

Ishizu, T., Amemiya, K., Yumoto, M., & Kojima, S. (2010). Magnetoencephalographic study of the neural responses in body perception. *Neuroscience Letters*, *481*(1), 36–40.

Jellema, T., & Perrett, D. I. (2003a). Cells in monkey STS responsive to articulated body motions and consequent static posture: A case of implied motion? *Neuropsychologia*, *41*(13), 1728–1737.

Jellema, T., & Perrett, D. I. (2003b). Perceptual history influences neural responses to face and body postures. *Journal of Cognitive Neuroscience*, *15*(7), 961–971.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*(11), 4302–4311.

Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*(6), 417–428.

Kiani, R., Esteky, H., Mirpour, K., & Tanaka, K. (2007). Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *Journal of Neurophysiology*, *97*(6), 4296–4309.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: Monkey and human FMRI studies. *Neuron*, *37*(2), 333–346.

Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., et al. (2008). Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron*, *60*(6), 1126–1141.

Lahnakoski, J. M., Glerean, E., Salmi, J., Jääskeläinen, I. P., Sams, M., Hari, R., et al. (2012). Naturalistic FMRI mapping reveals superior temporal sulcus as the hub for the distributed brain network for social perception. *Frontiers in Human Neuroscience*, *6*, 233. http://dx.doi.org/10.3389/fnhum.2012.00233.

Lamm, C., & Decety, J. (2008). Is the extrastriate body area (EBA) sensitive to the perception of pain in others? *Cerebral Cortex*, *18*(10), 2369–2373.

Liu, N., Kriegeskorte, N., Mur, M., Hadj-Bouziane, F., Luh, W. M., Tootell, R. B., et al. (2013). Intrinsic structure of visual exemplar and category representations in macaque brain. *Journal of Neuroscience*, *33*(28), 11346–11360.

Mather, G., Pavan, A., Bellacosa Marotti, R., Campana, G., & Casco, C. (2013). Interactions between motion and form processing in the human visual system. *Frontiers in Computational Neuroscience*, *7*, 65. http://dx.doi.org/10.3389/fncom.2013.00065.

Meeren, H. K.M, de Gelder, B., Ahlfors, S. P., Hämäläinen, M. S., & Hadjikhani, N. (2013). Different cortical dynamics in face and body perception: An MEG study. *PLoS One*, *8*(9), e71408. http://dx.doi.org/10.1371/journal.pone.0071408.

Meeren, H. K., Hadjikhani, N., Ahlfors, S. P., Hamalainen, M. S., & de Gelder, B. (2008). Early category-specific cortical activation revealed by visual stimulus inversion. *PLoS One*, *3*(10), e3503. http://dx.doi.org/10.1371/journal.pone.0003503.

Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(45), 16518–16523.

Minnebusch, D. A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. *Neuroscience & Biobehavioral Reviews*, *33*(7), 1133.

Moro, V., Urgesi, C., Pernigo, S., Lanteri, P., Pazzaglia, M., & Aglioti, S. M. (2008). The neural basis of body form and body action agnosia. *Neuron*, *60*(2), 235.

Oram, M. W., & Perrett, D. I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. *Journal of Neurophysiology*, *76*(1), 109–129.

Peelen, M. V., Atkinson, A. P., Andersson, F., & Vuilleumier, P. (2007). Emotional modulation of body-selective visual areas. *Social Cognitive and Affective Neuroscience*, *2*(4), 274–283.

Peelen, M. V., Atkinson, A. P., & Vuilleumier, P. (2010). Supramodal representations of perceived emotions in the human brain. *Journal of Neuroscience*, *30*(30), 10127–10134.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, *93*(1), 603–608.

Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, *8*(8), 636–648.

Perrett, D. I., Smith, P. A., Mistlin, A. J., Chitty, A. J., Head, A. S., Potter, D. D., et al. (1985). Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. *Behavioural Brain Research*, *16*(2–3), 153–170.

Pichon, S., de Gelder, B., & Grèzes, J. (2008). Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Social Neuroscience*, *3*(3–4), 199–212. http://dx.doi.org/10.1080/17470910701394368.

Author's personal copy

Pinsk, M. A., Arcaro, M., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., et al. (2009). Neural representations of faces and body parts in macaque and human cortex: A comparative FMRI study. *Journal of Neurophysiology*, *101*(5), 2581–2600.

Pinsk, M. A., DeSimone, K., Moore, T., Gross, C. G., & Kastner, S. (2005). Representations of faces and body parts in macaque temporal cortex: A functional MRI study. *Proceedings of the National Academy of Sciences*, *102*(19), 6996–7001, doi: 0502605102.

Pobric, G., & Hamilton, A. F. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology*, *16*(5), 524–529.

Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, *14*(4), 302–308. http://dx.doi.org/10.1111/1467-9280.14431.

Righart, R., & de Gelder, B. (2006). Context influences early perceptual analysis of faces: An electrophysiological study. *Cerebral Cortex*, *16*, 1249–1257.

Righart, R., & de Gelder, B. (2007). Impaired face and body perception in developmental prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(42), 17234–17238.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.

Rochat, M. J., Caruana, F., Jezzini, A., Escola, L., Intskirveli, I., Grammont, F., et al. (2010). Responses of mirror neurons in area F5 to hand and tool grasping observation. *Experimental Brain Research*, *204*(4), 605–615.

Saby, J. N., Meltzoff, A. N., & Marshall, P. J. (2013). Infants' somatotopic neural responses to seeing human actions: I've got you under my skin. *PLoS One*, *8*(10), e77905.

Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, *25*(47), 11055–11059.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, *115*(1), 15–36.

Sinke, C. B. A., Van den Stock, J., Goebel, R., & de Gelder, B. (2012). The constructive nature of affective vision: Seeing fearful scenes activates extrastriate body area. *PLoS One*, *7*(6), e38118.

Spiridon, M., Fischl, B., & Kanwisher, N. (2006). Location and spatial profile of category-specific regions in human extrastriate cortex. *Human Brain Mapping*, *27*(1), 77–89.

Stekelenburg, J. J., & de Gelder, B. (2004). The neural correlates of perceiving human bodies: An ERP study on the body-inversion effect. *Neuroreport*, *15*(5), 777–780.

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.

Thierry, G., Pegna, A. J., Dodds, C., Roberts, M., Basan, S., & Downing, P. (2006). An event-related potential component sensitive to images of the human body. *NeuroImage*, *32*(2), 871–879.

Thompson, J. C., Hardee, J. E., Panayiotou, A., Crewther, D., & Puce, A. (2007). Common and distinct brain activation to viewing dynamic sequences of face and hand movements. *NeuroImage*, *37*(3), 966–973.

Tsao, D. Y., Freiwald, W. A., Knutsen, T. A., Mandeville, J. B., & Tootell, R. B. (2003). Faces and objects in macaque cerebral cortex. *Nature Neuroscience*, *6*(9), 989–995. http://dx.doi.org/10.1038/nn1111.

Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences*, *105*(49), 19514–19519.

Tsunoda, K., Yamane, Y., Nishizaki, M., & Tanifuji, M. (2001). Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nature Neuroscience*, *4*(8), 832–838.

Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., et al. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences*, *105*(6), 2209–2213.

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *The Journal of Neuroscience*, *27*(30), 8023–8030.

van de Riet, W. A., Grèzes, J., & de Gelder, B. (2009). Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Social Neuroscience*, *4*(2), 101–120. http://dx.doi.org/10.1080/17470910701865367.

van den Stock, J., Righart, R., & de Gelder, B. (2007). Body expressions influence recognition of emotions in the face and voice. *Emotion*, *7*(3), 487–494.

Van den Stock, J., Vandenbulcke, M., Sinke, C. B., & de Gelder, B. (2014). Affective scenes influence fear perception of individual body expressions. *Human Brain Mapping*, *35*(2), 492–502.

van Heijnsbergen, C. C. R. J., Meeren, H. K. M., Grèzes, J., & de Gelder, B. (2007). Rapid detection of fear in body expressions, an ERP study. *Brain Research*, *1186*, 233–241.

Vangeneugden, J., Peelen, M. V., Tadin, D., & Battelli, L. (2014). Distinct neural mechanisms for body form and body motion discriminations. *Journal of Neuroscience*, *34*(2), 574–585.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron*, *30*(3), 829–841.

Wachsmuth, E., Oram, M. W., & Perrett, D. I. (1994). Recognition of objects and their component parts: Responses of single units in the temporal cortex of the macaque. *Cerebral Cortex*, *4*(5), 509–522.

Wallbott, H. G. (1998). Bodily expression of emotion. *European Journal of Social Psychology*, *28*(6), 879–896.

Weiner, Kevin S., & Grill-Spector, K. (2011). Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. *Neuroimage*, *56*(4), 2183–2199.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141–145.

Zieber, N., Kangas, A., Hock, A., & Bhatt, R. S. (2014). Infants' perception of emotion from body movements. *Child Development*, *85*, 675–684. http://dx.doi.org/10.1111/cdev.12134.