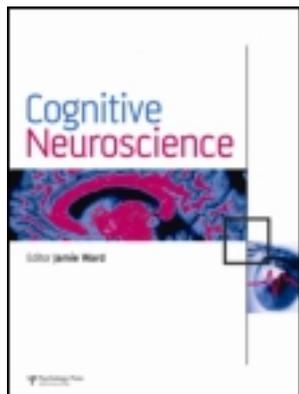


This article was downloaded by: [Richard Ramsey]

On: 01 November 2011, At: 07:54

Publisher: Psychology Press

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Cognitive Neuroscience

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/pcns20>

No two are the same: Body shape *is* part of identifying others

Richard Ramsey^{a b}, Hein T. van Schie^c & Emily S. Cross^{b c}

^a Faculté de Psychologie et des Sciences de l'Education, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

^b Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, Gwynedd, UK

^c Behavioural Science Institute, Radboud University, Nijmegen, The Netherlands

Available online: 01 Nov 2011

To cite this article: Richard Ramsey, Hein T. van Schie & Emily S. Cross (2011): No two are the same: Body shape *is* part of identifying others, *Cognitive Neuroscience*, 2:3-4, 207-208

To link to this article: <http://dx.doi.org/10.1080/17588928.2011.604721>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Discussion Paper

The role of occipitotemporal body-selective regions in person perception

Paul E. Downing¹ and Marius V. Peelen²

¹Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK

²Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy

The visual appearance of others' bodies is a powerful source of information about the people around us. This information is implicit in the stimulus and must be extracted and made explicit by the coordination of activity in multiple cortical areas. Here we consider the contribution to this process of two strongly body-selective occipitotemporal regions identified in human neuroimaging experiments: the extrastriate body area (EBA) and the fusiform body area (FBA). We address the evidence and arguments behind numerous recent proposals that EBA and FBA build explicit representations of identity, emotion, body movements, or goal-directed actions from the visual appearance of bodies, and also explore the contribution of these regions to motor control. We argue that the current evidence does not support a model in which EBA and FBA directly perform any of these higher-level functions. Instead, we argue that these regions comprise populations of neurons that encode fine details of the shape and posture of the bodies of people in the current percept. In doing so, they provide a powerful but cognitively unelaborated perceptual framework that allows other cortical systems to exploit the rich, socially relevant information that is conveyed by the body.

Keywords: Body perception; Extrastriate body area; Fusiform body area; Action perception; Emotional gestures; Self–other distinction.

The appearance of the human body provides important visual signals. We see some of our own movements, and to an extent these are guided visually. Visual body information also provides myriad social signals about other people—who they are, what they are doing, how they are feeling, and the like. Accordingly, the brain devotes considerable cortical resources to representing visual information about the human body (Berlucchi & Aglioti, 2010; Minnebusch & Daum, 2009; Peelen & Downing, 2007a; Schwoebel & Coslett, 2005). Clear evidence for specialized visual representations of the body—and a link between these and the temporal lobes—extends well into the previous century, and can be found in neuropsychology (Konorski, 1967) and in some of the earliest work on the visual response

properties of single units in the macaque temporal cortex (Gross, 1992).

Many of the more recent studies of the neural underpinnings of body perception in the human temporal lobes have converged around two strongly body-selective, focal regions of the human brain, identified with functional magnetic resonance imaging (fMRI) and confirmed with other methods. These are the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001) found in the posterior inferior temporal sulcus/middle temporal gyrus, and the fusiform body area (FBA) (Peelen & Downing, 2005a; Schwarzlose, Baker, & Kanwisher, 2005) found ventrally on the fusiform gyrus (Figure 1). The discovery of these regions has triggered a large volume and variety

Correspondence should be addressed to: Paul E. Downing, Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, Gwynedd LL57 2AS, UK. Email: p.downing@bangor.ac.uk

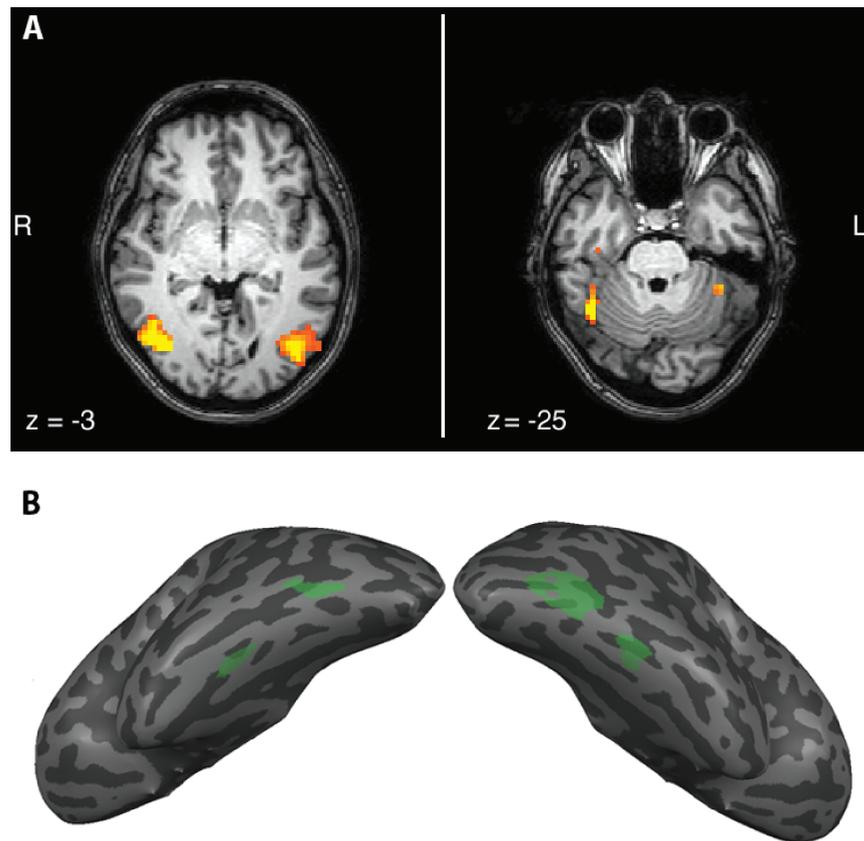


Figure 1. Location of occipitotemporal body-selective regions (extrastriate body area: EBA; fusiform body area: FBA). (A) EBA (left) and FBA (right) in one participant, defined by a contrast of bodies – (chairs + scenes), $p < .00005$. Z values refer to position of axial slices in Talairach space. (B) Results of a fixed-effects, group-average contrast of (bodies – chairs), $n = 8$, $p < .00001$, rendered on the inflated cortical surface of a single participant.

of subsequent work. This includes fMRI studies of healthy human populations and of psychiatric populations, and extends to investigations with transcranial magnetic stimulation (TMS), patients with neurological damage, event-related potential (ERP) and magnetoencephalography (MEG) techniques, and nonhuman primates.

We focus the present discussion on these two regions because they are clearly identifiable areas involved in visual body analysis, while acknowledging that they may be further subdivided by functional and/or anatomical criteria (e.g., Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010; Weiner & Grill-Spector, 2011), and that they must operate not in isolation but rather in concert with other brain areas. (We will return to these points later.) Now that there is a rich set of data about the properties of EBA and FBA, multiple research groups have proposed that their neural activity directly underpins a plethora of functions (Table 1). These include identifying other individuals, perceiving emotions, perceiving body movements, understanding the meaning of others' actions, and even the control of motor movements.

In our view, many of these proposals extend too far past the data. Here, we critically consider current evidence on the possible function(s) of EBA and FBA, with reference to a more parsimonious model: The extrastriate and fusiform body areas jointly create a detailed but cognitively unelaborated visual representation of the appearance of the human body. This representation makes explicit the aspects of the image that contain bodies or body parts, and represents their shape and posture in some detail. It does not, we argue, make explicit high-level information about other people, such as their identities, actions, or emotional states. Thus, this representation provides a general perceptual infrastructure that contributes to the information processing in other interconnected brain areas that extract complex and often context-dependent information about the people we observe.

BACKGROUND

Downing et al. (2001) reported new evidence from human fMRI for a lateral occipitotemporal region that

TABLE 1

The discovery of highly body-selective regions in the lateral (extrastriate body area; EBA) and ventral (fusiform body area; FBA) occipitotemporal cortex has led to a wide diversity of proposals for the functional role(s) that these regions play. The quotations below are taken out of context and are simply meant to illustrate this diversity. In this article, we argue, contrary to many (but not all) of these proposals, that these regions perform a role that is largely restricted to representing the shape and posture of the body, and it is not elaborated with information about identity, emotion, motion, action goals, or motor control

-
- Arzy et al. (2006): “Collectively, these data show that distributed brain activity at the EBA and TPJ as well as their timing are crucial for the coding of the self as embodied and as spatially situated within the human body.”
 - Astafiev et al. (2004): “Our results indicate that in addition to this visual recognition function, the EBA integrates visual, spatial attention, and sensory-motor signals involved in the representation of the observer’s body.”
 - Blanke et al. (2010): “Our data show that the EBA is also involved in mental imagery of human bodies.”
 - Calvo-Merino et al. (2010): “Our results suggest that the EBA and vPMC may be two complementary components of the aesthetic perception network for bodies.”
 - Chan et al. (2004): “We propose that the EBA plays a relatively early role in social vision.”
 - Costantini et al. (2005): “The higher BOLD signal during observation of impossible movements . . . not only suggests that EBA may be activated during action observation but also that this area codes body and action related stimuli multimodally.”
 - Cross et al. (2010): “A key function of EBA might be to extract body-form cues that are either unrelated, impossible or beyond what the viewer’s body can do.”
 - David et al. (2007): “Our results suggest that the EBA represents the human body in a more integrative and dynamic manner, being able to detect an incongruence of internal body or action representations and external visual signals.”
 - De Lange et al. (2008): “Our data show that EBA activity is further influenced by the motoric context in which the body part is presented.”
 - Downing, Peelen et al. (2006): “We speculate that the EBA computes a static representation of the human body and is not involved in analysis of biological motion *per se*.”
 - Hodzic, Muckli et al. (2009): “[Identity analysis] appears to be accomplished by a network comprising the right FBA, positioned ventrally to the EBA, regions of the superior parietal lobe, the inferior parietal cortex, and the middle frontal gyrus.”
 - Jackson et al. (2006): “It is thus likely that the EBA is important not only for the visual processing of body parts, but also for . . . automatically mapping the visual representation of another’s body to one’s own body.”
 - Jastorff & Orban (2009): “Our results suggest that the EBA and the FBA correspond to the initial stages in visual action analysis, in which the performed action is linked to the body of the actor.”
 - Kable & Chatterjee (2006): “Representations in the pSTS, MT/MST, and EBA abstract actions from the agents involved and distinguish between different particular actions.”
 - Kokal et al. (2009): “The presence of these regions [EBA and pSTS] in our [joint action] networks suggests that the process of integrating observed and executed actions . . . may also occur at a more sensory level.”
 - Kontaris et al. (2009): “In contrast to pSTS, EBA and FBA are decoupled from motor systems.”
 - Kuhn et al. (2011): “Our study suggests that both EBA and FFA play a role in the representation of one’s own body and in the control of voluntary action.”
 - Marsh et al. (2010): “The extrastriate body area may be geared to take into account the social meaning of actions, so that actions can be understood with reference to the person executing them.”
 - Moro et al. (2008): “Visual analysis of human body stimuli is based on the division of labor into two cortical systems, with EBA and FBA representing the actors’ identity and vPMC mapping the observed action in a neutral format with respect to the identity of the acting bodies.”
 - Myers & Sowden (2008): “We argue that the right EBA may perform an important sorting of body part images by identity (including self-recognition) and may interact both with brain areas involved in sensory processing and social cognition.”
 - Newman-Norlund et al. (2007): “EBA . . . may represent the brain basis of our ability to relate the movements of others directly with our own movements in joint-action situations.”
 - Pierno et al. (2009): “EBA . . . [has] a role concerned with the discrimination of specific aspects characterizing the observed actions.”
 - Pitcher et al. (2009): “Our results extend earlier findings by showing that rEBA represents bodies in their most common configuration.”
 - Pourtois et al. (2007): “[There is] a major role for EBA in the initial perceptual analysis of body shapes.”
 - Ramsey & Hamilton (2010): “Our data suggest that [FFA, EBA, FBA] are also recruited in more social and dynamic contexts; they distinguish between two intentional agents who are acting in a goal-directed fashion.”
 - Saxe et al. (2006): “[There is] a role for the right EBA in the perception of other people *per se*, perhaps as input to subsequent perception of others’ actions and reasoning about other minds.”
 - Suchan et al. (2010): “Body image distortion is related at least in part to structural alteration in the EBA.”
 - Urgesi, Candidi et al. (2007): “Thus, the present data clearly show that EBA is crucial in processing bodily forms but not bodily actions.”
-

responds strongly and selectively to images of human bodies and body parts. This followed earlier findings of similar face-selective (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996) and scene-selective (Aguirre, Zarahn, & D’Esposito, 1998; Epstein & Kanwisher,

1998) areas, and was part of a program to determine the extent of such apparently specialized regions (e.g., Downing, Chan, Peelen, Dodds, & Kanwisher, 2006). Several years after identifying EBA, we (Peelen & Downing, 2005a) identified a second highly body-selective region in the fusiform gyrus, overlapping, but

distinct from, the fusiform face area (FFA). Shortly afterwards, Schwarzlose et al. (2005) reported that high-resolution fMRI revealed a double dissociation between FBA and FFA.

fMRI studies have demonstrated that EBA and FBA respond to photorealistic depictions of whole human bodies or body parts, significantly more than to faces, face parts, objects, object parts, scenes, visual motion, and other control stimuli (Downing, Chan et al., 2006; Downing et al., 2001; Peelen & Downing, 2005a; Schwarzlose et al., 2005; Spiridon, Fischl, & Kanwisher, 2006; Weiner & Grill-Spector, 2010). The responses of these regions are not limited to full-cue stimuli: Their body selectivity extends to line drawings, “stick figures,” and silhouettes (Downing et al., 2001; Peelen & Downing, 2005a). The body representations in these regions appear to be viewpoint-dependent—in an fMRI adaptation design, changes in view greater than 45° result in release from adaptation to the level of a new stimulus (Taylor, Wiggett, & Downing, 2010). There is evidence from intracranial ERP for a body-selective visual response originating at the approximate site of EBA (Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007), and this is confirmed by scalp ERP (Thierry et al., 2006) and MEG (Ishizu, Amemiya, Yumoto, & Kojima, 2010) studies, and near infrared spectroscopy (Ishizu, Noguchi, Ito, Ayabe, & Kojima, 2009). Notably, fMRI, TMS, and ERP studies indicate that the representation of bodies in EBA is more strongly part-based than in FBA (Costantini, Urgesi, Galati, Romani, & Aglioti, 2011; Taylor, Wiggett, & Downing, 2007; Taylor, Roberts, Downing, & Thierry, 2010; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). Finally, recent fMRI studies of macaques show body-selective activation patches in the temporal cortex (Pinsk et al., 2005, 2009; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003), making an important link between human studies and previous single-unit work that reported strong selective neural responses to hands or whole bodies (Desimone, Albright, Gross, & Bruce, 1984; Gross, Bender, & Rocha-Miranda, 1969; Gross, Rocha-Miranda, & Bender, 1972; Oram & Perrett, 1996; Wachsmuth, Oram, & Perrett, 1994).

Is the response to human bodies and body parts in EBA and FBA functionally relevant for body perception? At least five published studies show a selective disruption to body- or body-part perceptual tasks following TMS over EBA (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Calvo-Merino et al., 2007; Urgesi, Candidi, Ionta, & Aglioti, 2007). These effects are specific to stimulus type and stimulation location, affecting only body perception (and not other

categories) and only when TMS is applied to EBA (and not other nearby areas). Further, a recent study of neuropsychological patients (Moro et al., 2008) found that impaired performance on body perception tasks was associated with lesions to areas that were consistent with EBA and FBA, and/or connections between these two regions (see also Kemmerer & Tranel, 2008; Schwoebel & Coslett, 2005). Taken together, these findings provide evidence that the activity in EBA and FBA plays a selective and causal functional role in some aspect(s) of body perception.

EBA and FBA are found close to, or overlapping with, other known regions. Thus, previous research has had to functionally distinguish these regions from their neighbors. For example, Downing et al. (2001) reported a dissociation between the responses of EBA and nearby motion-selective region hMT+ in the responses to moving objects and bodies (see also Pitcher et al., 2009; Spiridon et al., 2006; Valyear & Culham, 2010). Similarly, Peelen, Wiggett, and Downing (2006) used multivoxel pattern analysis (MVPA) (Haynes & Rees, 2006; Kamitani & Tong, 2005; Mur, Bandettini, & Kriegeskorte, 2009; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010; Peelen & Downing, 2007b) to distinguish the responses of motion-selective hMT+ and EBA to point-light biological motion stimuli (see also Downing, Wiggett, & Peelen, 2007). Most recently, Weiner and Grill-Spector (2011) used high-resolution fMRI to anatomically dissociate hMT+ and EBA. With respect to FBA, MVPA (Peelen et al., 2006), high-resolution fMRI (Schwarzlose et al., 2005), and developmental time course (Peelen, Glaser, Vuilleumier, & Eliez, 2009) show that the body-selective and face-selective responses in the fusiform gyrus can be dissociated. Importantly, this overlap means that occipitotemporal activations in the general region of EBA or FBA can be difficult to interpret without careful localization within-studies and within-participants (Figure 2).

The overlap and close proximity of EBA and FBA to other functional regions has further implications as well. For one, the nature of the neighboring areas may provide clues about the properties of EBA and FBA. For example, the proximity of EBA to motion-selective regions suggests that it interacts with dynamic visual representations, although we argue below that the body representation in EBA itself is not dynamic. Furthermore, very recent evidence suggests that the highly body selective responses we define as EBA and FBA may be situated in a much broader, more weakly body-sensitive expanse of cortex. Specifically, Orlov, Makin, and Zohary (2010) find large occipitotemporal regions that respond subtly but reliably more to specific body parts (e.g., upper or lower limbs) than to other body parts. Both of these observations provide an important context for

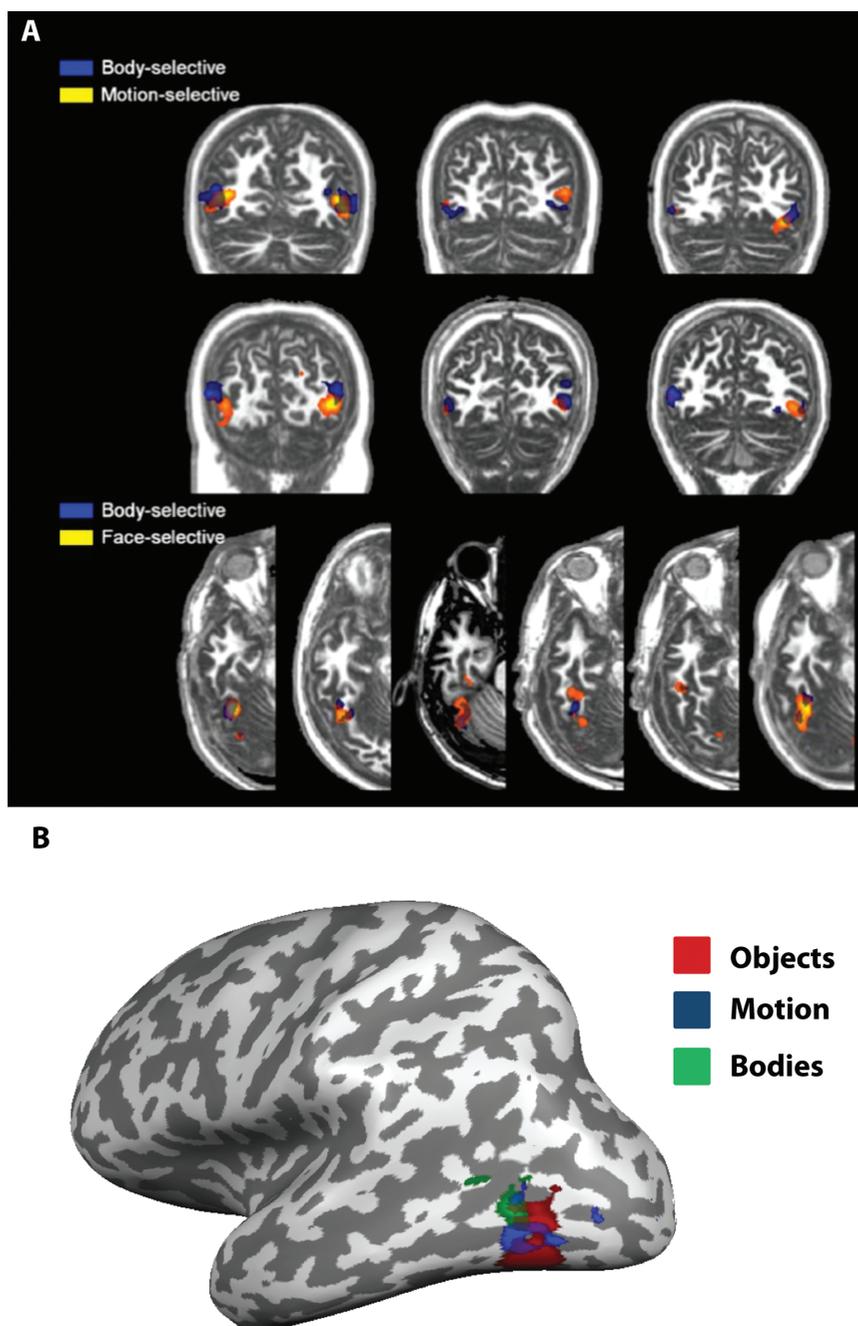


Figure 2. Overlap of functionally defined EBA and FBA and neighboring regions. (A) Overlap in six individual participants (at $p < .001$), adopted from Peelen et al. (2006). Upper panel shows overlap between extrastriate body area and motion-selective hMT+. Lower panel shows overlap between fusiform body area and fusiform face area. (B) Schematic illustration of the overlap of body-, object-, and motion-selective regions, rendered on the inflated cortical surface of a single participant. Random-effects, group-average analysis, $n = 14$, $p < .001$ (bodies), $p < .0001$ (motion), $p < .00001$ (objects). Results like these highlight the necessity for functional localization of regions of interest in studies of extrastriate visual areas.

understanding EBA and FBA and we consider them further in the concluding section.

We make a last note on interpreting fMRI results before turning to a review of the evidence. At several points in the following discussion, we attribute modulations of activity in EBA or FBA to (often

unintended) variations in the degree to which selective attention is allocated to bodies or body parts in the stimulus. Many studies have shown attentional modulation in retinotopic visual cortex (Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Kastner, De Weerd, Desimone, & Ungerleider, 1998)

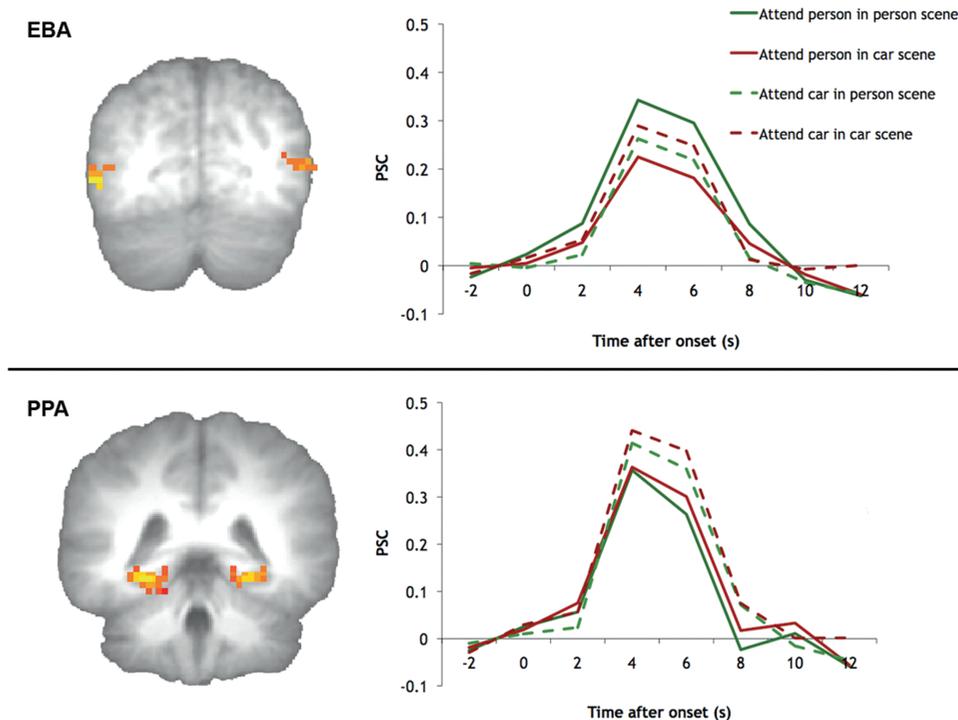


Figure 3. Event-related time courses in EBA (top) and PPA (bottom) in response to pictures of natural scenes. The scenes could contain persons or cars, and participants were instructed to attend (in different runs) to one of these categories. When attention was directed to persons (solid lines), responses in EBA showed stronger responses to scenes containing persons than to scenes containing cars (green solid line higher than red solid line). By contrast, when attention was directed to cars (dashed lines), no selective response to person scenes was observed (no difference between green dashed line and red dashed line). These results show that top-down attention can strongly modulate responses in EBA. The interaction between attention and scene content was specific to body-selective regions and was not observed in PPA (bottom). For more analyses and information, see Peelen et al. (2009).

as well as in high-level extrastriate areas such as the parahippocampal place area (PPA) (Epstein & Kanwisher, 1998), FFA, and hMT+ (e.g., O’Craven, Downing, & Kanwisher, 1999; O’Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Wojciulik, Kanwisher, & Driver, 1998). On these grounds, it is highly likely that varying attention to body or body part stimuli will have congruent effects on the responses of EBA and FBA. Consistent with this, Morris, Pelphrey, and McCarthy (2006) found that the EBA activity elicited by bodies was reduced when a face was present in the image, compared to when there was not. A simple attentional account of these findings is that when a face is present, it is spatially attended (or fixated) at least some portion of the time, and the net effect on EBA response is suppressive (given the low response in this region to faces presented alone; Downing et al., 2001). Further direct evidence is found in recent data from Peelen, Fei-Fei, and Kastner (2009). In that study, participants were required to attend to either people or cars in briefly presented natural scenes. Activity in EBA, but not scene-selective PPA, was modulated by the task set, such that selectivity for bodies (vs. cars) was stronger

during the body task than the car task (Figure 3). These category-based attention effects were highly robust, and were found for both spatially attended and unattended pictures. This means that where experimental manipulations confound how much spatial or nonspatial attention is focused on body stimuli, the interpretation of results may be compromised.

FIVE POSSIBLE FUNCTIONS FOR BODY-SELECTIVE EXTRASTRIATE REGIONS

The following discussion is organized into five sections, each describing a possible role of EBA and FBA in body representation: perceiving identity, perceiving emotion, perceiving body motion, perceiving actions and goals, and motor control. For many of these functions, researchers have claimed that EBA or FBA perform complex, elaborate roles (Table 1); for example, they claim that these regions “understand” others’ actions, or coordinate one’s own behavior with that of another individual. We will argue that the findings that were taken as support for these claims can be more

parsimoniously explained by a model in which EBA and FBA represent visual features of the body such as shape and posture without further elaboration.

Perceiving identity

Although person identity is often perceived from facial cues, the rest of the body also provides important information about identity. Body posture, shape, and gait can all be used to determine person identity, and may be particularly useful when the face is poorly visible such as when viewing someone from behind or at a distance. Since recognizing identity from bodies requires the perceptual analysis of body stimuli, it is likely that EBA and FBA play an important role in this process. Below, we discuss studies that have investigated the role of EBA and FBA in extracting person identity, and indicate how a perceptual account of these regions can accommodate these findings.

Several studies have investigated whether EBA and FBA respond differentially to images of one's own versus another person's body, as this is perhaps the most fundamental identity distinction. Chan, Peelen, and Downing (2004) reported no difference between EBA responses elicited by viewing the bodies of the self versus familiar others in a blocked design fMRI experiment. Subsequent studies that contrasted the self with familiar others similarly found no difference in EBA or FBA (Devue et al., 2007; Hodzic, Kaas, Muckli, Stirn, & Singer, 2009), although one study (that did not localize EBA/FBA) reported a broad swath of occipitotemporal cortex that responded more to self than to familiar other images (Sugiura et al., 2006). The results of studies that contrasted images of the self with *unfamiliar* others are less consistent: Hodzic, Kaas et al. (2009) found no difference in right EBA, but a stronger response to self than other bodies in left EBA and right FBA. However, in another study, these authors did not find a difference between self and unfamiliar other in EBA or FBA (Hodzic, Muckli, Singer, & Stirn, 2009). Finally, Vocks et al. (2010) reported small but significant increases to own bodies relative to unknown others' bodies in right EBA and FBA.

Thus, while most studies reported no difference in EBA and/or FBA between self and other bodies, some studies reported modest increases in one or both of these regions. It should be noted that these studies compared the overall BOLD signal in EBA and/or FBA to images of the self versus a familiar or unfamiliar other. It is unlikely, however, that a region that extracts identity from perceived bodies would show gross differences in the overall response magnitude to different identities.

More likely, different identities would elicit different patterns of activity resulting in roughly the same gross level of response (Kriegeskorte, Formisano, Sorger, & Goebel, 2007). So these studies may not be ideally suited to test whether EBA/FBA represents identity. Rather, they test whether EBA and FBA are primarily involved in representing the self (e.g., for guiding actions) or the other (e.g., for social cognition)—and their results do not point to a uniquely strong role in either process.

Another approach to test whether EBA and/or FBA primarily encode the self or the other is to test the effect of viewpoint: If EBA/FBA would preferentially respond to one's own body parts, we would expect a stronger response to body parts presented in a first person viewpoint (camera at eye level), while stronger responses to third person views would be expected if these regions are primarily involved in the encoding of others' bodies. The two studies that have manipulated viewpoint both found slightly stronger responses in right EBA to bodies presented in third person view (Chan et al., 2004; Saxe, Jamal, & Powell, 2006), inconsistent with the preference for one's own body reported by some of the studies reviewed above.

Using a blocked-design adaptation approach, Myers and Sowden (2008) reported significantly stronger responses (i.e., less adaptation) in right, but not left, EBA (FBA was not tested) to blocks in which images of the participants' own hand were alternated with images of an unknown other's hand, relative to blocks where two other individuals' hands were alternated. The authors concluded that right EBA contains different neural populations to represent the appearance of one's own versus others' body parts. These results may alternatively be explained by differences in attention: It is not unlikely that participants paid more attention to their own hands than to a stranger's hand, especially because the participants' own body parts appeared relatively infrequently in the experiment. Such attention effects would be expected to primarily modulate higher-level visual areas strongly responsive to the hand stimuli, rather than weakly responsive areas or lower-level visual cortex.

Perceiving identity is, of course, not limited to distinguishing the self from others. Surprisingly, only a few studies have investigated the role of EBA or FBA in representing body identity beyond the self/other distinction. Kable and Chatterjee (2006) used a long-term, event-related adaptation design, with dynamic whole-body/face stimuli, to investigate adaptation to actor identity. No significant identity adaptation was found in EBA. In a subsequent extension of this study, the absence of significant identity-related adaptation effects in EBA and FBA was confirmed (Wiggett & Downing, 2010). Ramsey and Hamilton (2010) also

used an adaptation design with the similar aim of examining representations of actors. Functional localization was not performed, but anatomical regions of interest around fusiform and middle temporal gyri (and other areas) were tested with small-volume correction analyses. Both areas showed significant adaptation for repeated versus nonrepeated actors, which the authors attributed to “person identity processes” taking place in EBA and FBA. However, it is not clear which aspect of the stimulus drove this adaptation—whether it was the repetition of actor identity, the repetition of body shape, or the repetition of low-level visual aspects such as the color of the clothes.

Together, these results suggest that EBA and FBA are involved in the encoding of body parts belonging to the self as well as to others. Small modulations reported in some of the studies reviewed here may be explained by attentional differences—looking at a picture of yourself may simply be more interesting than looking at a picture of a stranger. Notably, identity effects tend to be found when identity is either an explicit part of the participants’ task (Hodzic, Kaas et al., 2009; Ramsey & Hamilton, 2010; Sugiura et al., 2006) or else is made explicit to participants by direct cues (Vocks et al., 2010). This pattern points strongly to the idea that identity modulation in EBA or FBA is the result of top-down influences, including attentional biases.

What could be the role of EBA and FBA in the perception of body identity? We argue that the role of these regions consists in creating a perceptual representation of the shape and posture of the body and its parts, which may then be used by other brain regions (e.g., the anterior temporal lobes; Kriegeskorte et al., 2007) to represent person identity explicitly. On this account, EBA and FBA encode body identity only in the sense that these regions differentiate between individuals with different body shapes. We argue that EBA and FBA do not, however, explicitly represent person identity beyond body shape, and as such may not specifically differentiate between the bodies of the self and others. While identity can be extracted from body shape, identity and shape can be dissociated (people age, grow, lose or gain weight, undergo plastic surgery, etc.). Furthermore, identity can be extracted from multiple body parts (e.g., lower and upper body). We expect responses in EBA/FBA to follow the perceived body shape (or body part) rather than the perceived body identity.

Note that our account does not exclude the possibility that responses in EBA and FBA can be influenced by identity through top-down modulation: The sight of a romantic partner (or, indeed, the self) may increase responses in EBA/FBA due to increases in attention and arousal. Also, we expect that familiarity with

particular body shapes (e.g., growing up in a country with tall people) may change the tuning of body-selective neurons, such that their discrimination of body shapes is optimal for the current environment. Finally, the knowledge of another person’s body shape (available after identifying the person, whether through visual or nonvisual cues) may modulate responses in EBA and FBA, as, for example, in cases where clothes obscure most of the body. In other words, responses in EBA and FBA are not merely a copy of the visual image, but more closely correspond to the subjective percept, which is influenced by identity (and other factors). The critical test of our account would require an experiment that dissociates body shape and body identity in combination with suitable techniques (e.g., MVPA). Distributed activity in EBA and FBA should conform to a “space” in which different body shapes/parts, but not necessarily different individuals, are represented by systematically different corresponding patterns.

Perceiving emotion

Basic emotions, such as fear, anger, and happiness, are associated with characteristic body postures and movements (Atkinson, Dittrich, Gemmell, & Young, 2004). Apart from providing information about others’ emotional states, bodies may also evoke emotions in the observer—for example, through empathy (e.g., with others’ pain), admiration of beauty (e.g., in dance), or sexual arousal. What is the role of occipitotemporal body-selective areas in these processes? Here we consider the evidence from studies that have implicated EBA or FBA in the processing of emotion from body stimuli.

Research on emotional body perception has largely addressed questions that had earlier been addressed in the field of emotional face perception, such as comparing fMRI responses to emotional expressions with responses to neutral expressions. Employing this approach, research on face perception indicates that emotional expressions modulate responses in visual cortex, particularly the fusiform face area (for a review, see Vuilleumier, 2005). These emotional modulations are similar to attentional modulations but are thought to be mediated by the amygdala, rather than by frontoparietal attention networks (Amaral, Behnia, & Kelly, 2003; Morris et al., 1998; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Such activity increases in visual cortex may correspond to the enhanced perceptual processing of emotionally salient stimuli (e.g., Anderson, 2005).

Similar to emotional faces, emotional bodies have been shown to modulate perceptual responses, with

increased visual cortex (and amygdala) activation to arousing body expressions such as fear (Hadjikhani & de Gelder, 2003). A large number of studies from multiple laboratories have replicated these effects, using various emotions and both static and dynamic body stimuli (e.g., Carter & Pelphrey, 2008; Flaisch, Schupp, Renner, & Junghofer, 2009; Grezes, Pichon, & de Gelder, 2007; Grosbras & Paus, 2006; Kret, Pichon, Grezes, & de Gelder, 2011; Nummenmaa, Hirvonen, Parkkola, & Hietanen, 2008; Peelen, Atkinson, Andersson, & Vuilleumier, 2007). Although it is beyond the scope of this paper to review these studies in depth, a few general observations emerge from this literature. For example, it seems that arousal rather than valence is driving emotional modulation, since no modulation was found for bodies expressing sadness (Peelen et al., 2007). Further, emotional modulation has been primarily, but not exclusively, reported in body-selective parts of visual cortex (i.e., at the location of EBA and FBA), with some studies (mostly those using static body postures with blurred faces) finding stronger modulation in fusiform gyrus (presumably FBA) than at the location of EBA (e.g., Van de Riet, Grezes, & de Gelder, 2009). In a study using dynamic body expressions, it was shown that emotional modulation is proportional to static body selectivity (measured in a separate localizer scan) across the voxels of EBA and FBA, with the strongest modulation observed in voxels with the strongest body selectivity (Peelen et al., 2007). In the same study, emotional modulation in EBA and FBA was shown to correlate with emotion-driven increases in the amygdala, again highlighting the similarity between the mechanisms involved in emotional body and face processing (Peelen et al., 2007). Finally, modulation in visual cortex (including putative body-selective regions) has also been reported for sexually arousing body stimuli (Cikara, Eberhardt, & Fiske, 2011; Hamann, Herman, Nolan, & Wallen, 2004; Mouras et al., 2003; Ponseti et al., 2006).

Together, these results suggest that activity increases in EBA and FBA in response to emotional or sexual body stimuli primarily reflect modulatory effects (or “emotional attention”), rather than a direct encoding of emotions within these regions. It should be noted, however, that (as far as we know) no study has directly tested for explicit representations of emotions in these regions, as by using fMRI adaptation or MVPA (cf. Peelen, Atkinson, & Vuilleumier, 2010).

Observing someone else’s body in acute physical pain can hurt, especially when this person is a loved one. This empathy for others’ pain has been shown to activate regions in the anterior insula and anterior cingulate cortex, regions that also activate when one is

directly experiencing pain (Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Singer et al., 2004; but see Morrison & Downing, 2007). Although body-selective regions have not been implicated in the direct experience of pain, they may play a role in the perception of pain in others. For example, Singer et al. (2004) found activity in fusiform gyrus as well as more posterior visual regions in response to observing another’s hand that is thought to be in pain (as indicated by a symbolic cue) relative to when this hand was known not to be in pain. Similarly, Gu et al. (2010) found increased responses in occipitotemporal regions (probably including EBA) to photographs of body parts in painful daily-life incidents. However, such pain-related modulation was not observed in several other studies that showed a needle or knife touching a hand or foot (Benuzzi, Lui, Duzzi, Nichelli, & Porro, 2008; Morrison et al., 2004; Morrison, Peelen, & Downing, 2007). The only study to directly investigate pain-related responses in functionally localized EBA also used images showing a needle contacting a hand. No modulation was found in EBA, and it was concluded that the EBA is not relevant for empathy (Lamm & Decety, 2008). Thus, although there is currently no direct evidence that body-selective regions are modulated by observed pain, several studies suggest this might be the case for some stimuli. Studies that used stimuli in which a noxious object interacts with a body part (e.g., a needle contacting a hand) typically failed to find modulation in visual cortex. A possible explanation could be that in these studies participants directed attention toward the noxious object, or toward the local site of impact, rather than the body part. Such differences in attentional focus could have offset any pain-related modulatory effects.

There is a strong emotional aspect to clinical eating disorders such as anorexia nervosa and bulimia nervosa, in that patients may react with strong negative feelings toward the appearance of their own bodies or to others they perceive as overweight. These disorders can be associated with distortions of the body image, as revealed in misperceptions of body shape and size, and hence some authors have made a connection between these syndromes and EBA or FBA. Uher et al. (2005; see also Aleong & Paus, 2010; Sachdev, Mondraty, Wen, & Gulliford, 2008) tested visual responses to body images in patients and in control participants. Line drawings of women in either underweight, normal, or overweight versions were compared in a blocked-design fMRI experiment. Low body selectivity was seen in occipitotemporal cortex in patients relative to controls. Furthermore, in a fusiform region, patients showed reduced activity (relative to controls) for the overweight stimuli, and increased activity for

the underweight stimuli. In a study of functional and structural neuroanatomy, Suchan et al. (2010) identified EBA in anorexia patients and healthy controls, who also performed a behavioral test in which they estimated their own body sizes against a set of standardized silhouettes. Whole-brain voxel-based morphometry showed a reduction in gray matter volume in the patients, relative to controls, narrowly restricted to a region that fell in the functionally defined left EBA. Further, there was a negative relationship between anatomy and behavioral performance: Greater error on the body size judgment task was related to lower gray matter volume in EBA. Together, findings such as these suggest that eating disorders may be associated with distorted perception of bodies, or reduced or altered attention to bodies, and these characteristics may be related to differences in structural neuroanatomy in or around EBA.

Finally, a recent study used TMS to investigate the role of EBA in the aesthetic evaluation of dance postures (Calvo-Merino et al., 2010). TMS over EBA reduced aesthetic sensitivity (i.e., aesthetic judgments were less consistent) for body stimuli, but not for control stimuli, relative to TMS over ventral premotor cortex. Since the differences between the dance postures were related to changes in limb position, a reduction of aesthetic sensitivity would be expected if the perceptual processing of limb position was disrupted by TMS over EBA. As such, this study does not provide evidence that EBA is specifically involved in aesthetic evaluation beyond the perceptual representation of body posture.

To conclude, there is convincing evidence that emotional and sexual body stimuli (vs. neutral bodies) can modulate processing in body-selective regions in occipitotemporal cortex. These modulatory effects of emotion are likely to be similar to the effects of attention, in that they increase the strength of perceptual representations, but may have a different cortical origin than visuospatial attention effects. No evidence currently exists for a role of EBA or FBA in the direct representation of emotions beyond the perceptual representation of body shape and posture.

Perceiving body motion

The human body is nearly always moving, and this results in characteristic patterns of visual motion. So it is to be expected that visual motion will be a critical component of the neural representation of the body. Indeed, given the close proximity of EBA to motion-selective area hMT+ (Downing et al., 2007), a plausible account of body-selective responses in EBA would be that these reflect selectivity to body movements

(either implied by the stimulus or directly depicted) rather than body shape. Perhaps counterintuitively, then, there is accumulating evidence that the body representations in EBA and FBA are not dynamic: that is, they do not explicitly represent the motions of body parts.

Downing et al. (2001; see also Beauchamp, Lee, Haxby, & Martin, 2002) manipulated the combination of object kind and motion cues in order to test whether EBA shows a particularly strong response to characteristic human motions. Objects and bodies were presented either statically, with simple rigid motion, or with realistic dynamic motion. In EBA, increasing responses were seen from static to rigid to dynamic body stimuli, but the same pattern was found for objects as well, suggesting a general effect of motion complexity that was not specific to body processing.

Rather than use full-cue stimuli, however, much of the work on perception of human motion has made use of variants on Johansson's (1973) "point-light" stimuli, which can convey the patterns of biological motion in the absence of surface form (see Blake & Shiffrar, 2007). Grossman and Blake (2002) reported that EBA did not respond selectively to point-light displays of various whole-body movements, relative to scrambled controls. However, in later experiments, such effects were demonstrated and were extended to FBA (e.g., Michels, Kleiser, de Lussanet, Seitz, & Lappe, 2009; Michels, Lappe, & Vaina, 2005; Peelen et al., 2006; Peuskens, Vanrie, Verfaillie, & Orban, 2005). For example, Peelen et al. (2006) found greater responses in the fusiform gyrus and inferior temporal sulcus to intact versus scrambled whole-body point-light actions. Using MVPA, we showed that the degree of selectivity for these animations correlated positively, voxel-by-voxel, with the degree of selectivity for static body images in these regions (and not with motion or face selectivity). We argued that the "biological motion" response of EBA and FBA should be attributed to the percept of a body *per se* (which is elicited by structure from motion in intact point-light animations), and not to an explicit representation of patterns of biological motion.

Jastorff and Orban (2009), however, have argued to the contrary. They tested the responses of EBA and FBA to point-light animations of whole-body movement in a 2×2 design. The individual points moved either with realistic patterns of biological movement, or translated rigidly as a group. Further, they were either configured to conform to the shape of a human body (e.g., points at key joints) or not. In EBA and FBA, an interaction was found: responses were maximal when the motion type was biological and the configuration of points was intact. Jastorff and Orban (2009) argued that

form and motion interact in these regions; that is, that the neural representations in EBA and FBA encode dynamic aspects of movement explicitly. However, it is only in the intact configuration/intact motion condition that body structure is apparent. Without realistic patterns of biological movement, the body-like structure implicit in a rigidly moving pattern of points is very weak. On these grounds, the results of Jastorff and Orban (2009) are instead consistent with our proposal that it is body structure, rather than biological motion *per se*, that is encoded in EBA and FBA.

Static stimuli can strongly imply motion and can engage motion-processing mechanisms: Consider a snapshot of a sprinter taken as she bursts from the starting blocks. This effect is captured in the “representational momentum” phenomenon (Kelly & Freyd, 1987), in which static images of an object in motion are subsequently recalled as if the object had continued traveling in the depicted direction. In a comparison of “active” (e.g., alert and ready to perform a movement) and “passive” (e.g., resting) whole-body postures, Downing et al. (2001) found no modulation of activity in EBA. The same manipulation, however, significantly modulates activity in nearby hMT+ (Kourtzi & Kanwisher, 2000; but see Lorteije et al., 2010) suggesting that that region, but not EBA, is sensitive to implied motion.

In sum, we argue that the body representations in EBA and FBA are related to the shape of the body and not the visual stimulation produced by its movements. Shape information can be extracted from biological motion cues, thereby activating EBA and FBA when the perceived shape is a body or body part. Explicit representations of human body movements are extracted elsewhere in the brain. Extensive evidence from many methods points to the superior temporal sulcus as a key region for representing the patterns of human movement and perhaps for extracting meaningful cues such as direction of attention or intentions (Allison, Puce, & McCarthy, 2000; Puce & Perrett, 2003; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004).

Given that the body is nearly always in motion, and that it moves in such regular, characteristic, and often meaningful ways, it remains puzzling that static representations of the body form should be neuroanatomically distinct from the regions that extract dynamic information. Notably, distinct static and dynamic representations (of body shape and characteristic movements, respectively) have been incorporated into formal models of biological motion perception and gesture understanding (Giese & Poggio, 2003; Lange & Lappe, 2006; Peigneux et al., 2004). A common element of these models is that known body

movements may be represented by static “snapshots,” representing the elemental postures that characterize a movement (see also Singer & Sheinberg, 2010, for evidence from macaques). Interestingly, some computer animation software creates realistic human movement by allowing the user to specify static key frames and then rendering the movements by interpolating between these. There may be a useful analogy in the coarse-coding principle (Hinton et al., 1986), under which, for example, a wide range of line orientations can be coded efficiently by a weighted combination of detectors optimized for only a small set of orientations (e.g. horizontal and vertical). Similarly, the range of human movements may be usefully coded by reference to a “library” of commonly seen static poses that can be used combinatorially.

New experiments could test whether some postures are more likely (on behavioral or computational grounds) to act as “key frames” in the perception of movement, and whether these poses are represented specially in EBA and FBA. Furthermore, the results from studies of static images (Taylor et al., 2007) suggest a bias for local body parts in EBA relative to larger assemblies of parts in FBA, leading to the prediction that these areas contribute differently to representing movements of parts and wholes. Finally, computational studies will need to explicitly compare families of models that do or do not include static body representations, in order to see how they fare at predicting behavioral performance, and the activity in EBA and FBA, on relevant tasks.

Perceiving actions and goals

Perception of the dynamic aspects of human motion can be an end in its own right, or an initial step in the more general process of understanding the meaning, intentions, and goals behind others’ actions (e.g., Grafton & Hamilton, 2007). However, understanding the actions of others does not necessarily require dynamic motion cues, as actions can be rapidly understood from static images as well (Bach, Peelen, & Tipper, 2010; Johnson-Frey et al., 2003). Thus, although occipitotemporal body-selective areas do not explicitly encode body motion, they might nonetheless contain representations of others’ actions. To what extent are these areas involved in differentiating body actions? And do they take into account the surrounding context (e.g., objects, other people) of an action, or the inferred goals of the actor, when creating a body representation?

Urgesi, Candidi et al. (2007) presented static body part stimuli in a delayed match-to-sample task. The

images could vary either in the action they implied (subtle variations in the position of appendages) or form (subtle variations in their shape). TMS over EBA impaired performance on the form task, but not the action task, while TMS over ventral premotor cortex produced the opposite pattern (see also Pitcher et al., 2009). These findings suggest that EBA does not critically contribute to representing actions implied from static images. This is consistent with the findings of Downing, Peelen, Wiggett, & Tew (2006), who broke movies of whole-body movements into static frames and manipulated the order in which these were presented. In the coherent condition, the frames were presented in the original order, to create a meaningful action sequence without motion cues. In the incoherent condition, frames from different actions were mixed, leading to a disjointed percept and to relatively large frame-to-frame differences. Posterior STS and frontoparietal areas responded more to the coherent series, suggesting they represented the unfolding coherent actions. However, EBA (and to some extent FBA) responded more strongly to the incoherent than to the coherent series. These results again suggest that EBA and FBA do not form an integrated representation of body actions.

Many everyday actions are object directed, as in the use of tools or other implements. Does activity in EBA or FBA reflect the relationship between the movement and the object? De Lange, Spronk, Willems, Toni, and Bekkering (2008) found increased bilateral activity in a region they attributed to EBA (not localized) when participants observed atypical versus typical object-directed actions (e.g., drinking from a cup with a typical grasp or a clumsy, backwards grip). They argue that this shows EBA is sensitive to the “motoric context” in which body parts are viewed. When Valyear and Culham (2010) took a similar approach—comparing the observation of typical versus atypical grasps of tools—they found a left posterior middle temporal gyrus region that was sensitive to grasp. Notably, this effect did not extend to functionally defined EBA. In that study, however, both types of grasp did produce a greater response in right EBA than a control condition that showed an object simply being touched. Likewise, Pierno et al. (2009) found an increased occipitotemporal response to grasping (over pointing) movements, which they attributed to EBA. Both effects could simply reflect competition between stimuli—in grasp, but not point, conditions, less of the target object is visible, and hence that object makes a weaker competitor for attention with the hand stimulus. Moreover, grasp actions may direct attention to the object more strongly than pointing (Bekkering & Neggers, 2002), with the same result on activity in EBA.

Several recent studies compared the effects of attending to different aspects of actions. For example, Spunt, Satpute, and Lieberman (2011) had participants view movies of short, object-directed actions under different task instructions. Increased activity was seen in left lateral occipitotemporal cortex when participants covertly attended to the mechanics of the actions (“how”) rather than to the descriptive (“what”) or intentional (“why”) aspects. The authors argue (and we agree) that this could reflect increased attention to the body under “how” instructions (since perceiving the body accurately is essential to understanding the mechanism of an action). In contrast, understanding “why” an action takes place will naturally require wider attention to other aspects of the surrounding scene.

A visual-attention account does not explain, however, why similar lateral occipitotemporal activations are found in studies that use purely verbal material. Such studies aim to test an “embodied” view of action knowledge, whereby even abstractly specified concepts (e.g., words about actions) are rooted in the activity of visuomotor brain areas. Spunt, Falk, and Lieberman (2010) had participants make “how” (relative to “why”) judgments about actions described verbally. Likewise, Van Dam, Rueschemeyer, and Bekkering (2010) compared the reading of verbs that were generic with respect to a motor program (e.g., “to clean”) and verbs that were more closely tied to actions (e.g., “to wipe”). And Rueschemeyer, Pfeiffer, and Bekkering (2010) compared nouns related to actions made toward the body (e.g., cup, comb, sweater) with “world-” related items that typically involve actions away from the body (e.g., wrench, pen, frisbee). All of these studies identified lateral occipitotemporal activations (variably on the left or right), and these were attributed directly to EBA by Van Dam et al. (2010) and Rueschemeyer et al. (2010).

Such results could reflect semantic or crossmodal action or body knowledge in EBA. Alternatively, they could reflect top-down activation of perceptual body representations—for example, through mental imagery or automatic association processes—after the meaning of the words has been processed elsewhere. Furthermore, the relationship of these activations to EBA is unclear, as none of these studies localized this area functionally—and the candidate regions in Van Dam et al. (2010; Figure 1, Table 3) make a particularly poor match to EBA on anatomical grounds. This is important, as noted above and illustrated in this context by the findings of Valyear and Culham (2010), because without precise localization, EBA may be confused with nearby areas with entirely different functional properties (see also Takahashi et al., 2008). Results of

a recent study examining the lateral occipitotemporal responses to reading various categories of words (including nouns and verbs) emphasize this point. Bedny, Caramazza, Grossman, Pascual-Leone, and Saxe (2008) found that these verbal stimuli deactivated EBA (which was independently localized) relative to baseline, and further that there was no differentiation among word categories in that region.

All of the above studies measured gross changes in the level of activation in occipitotemporal cortex. The logic of repetition suppression (e.g., Grill-Spector, Henson, & Martin, 2006) may be more suited to detecting neural populations that encode perceived actions. This approach was first applied to EBA by Kable and Chatterjee (2006), who found that activity in a number of areas, including functionally defined EBA, was reduced when participants viewed a short movie of an action that had been seen previously in the experiment, compared to a new action. This repetition suppression effect was seen even when the actor involved in the two presentations was different, suggesting adaptation of an action representation at a relatively generic or semantic level. However, in a replication and extension, Wiggett and Downing (2010) found that this action priming effect was widespread—extending across face, object, scene, and body selective regions of interest in the lateral and ventral occipitotemporal cortex—and could not be attributed specifically to body-specific regions. Instead, it may reflect more general consequences of repetition, such as reduced attention arising from familiarity.

In summary, as we consider increasingly abstract aspects of actions, such as the objects they are directed to, their meaning, and the purpose of the actor in performing them, the relevant neural codes naturally move further away from a specific description of the posture and shape of the actor. Very similar movements can carry out very different goals (e.g., a gentle touch vs. a nasty poke), and, conversely, very different movements can achieve the same outcome (e.g., Umiltà et al., 2008). When stimulus and attentional differences, and functional localization, are taken into account, we find little evidence to support the proposal that the representations of EBA and FBA can make the kinds of distinctions necessary to support high-level action understanding. Rather, as many authors have described elsewhere (e.g., Van Overwalle & Baetens, 2009), the evidence points to prefrontal and especially parietal regions as key for this process. It is likely that the information provided by EBA and FBA—particularly about body posture (Downing, Peelen, et al., 2006)—provides an important part of the input to these areas, which can in turn integrate this with input from other neural sources in order to incorporate the

contextual information that is key to understanding actions.

Motor control

Movements of the body are coordinated by the joint activity of the frontal and parietal cortices and the cerebellum. However, the finding that extrastriate occipitotemporal areas respond to images of the body naturally raises the question of whether these areas also play some role in motor control (Downing et al., 2001). While they are unlikely to directly control the activity of muscles, these regions could be critically involved in visuomotor coordination by providing online visual tracking of the positions of one's own limbs. Alternatively, signals from the motor system could directly modulate the responses of neurons in these regions, perhaps to anticipate the visual consequences of body-part movements. Thus, the strongly visual response of EBA and FBA does not rule out *a priori* a role in motor behavior, or interactions with the motor system.

The first direct test of a motor role for EBA was conducted by Astafiev, Stanley, Shulman, and Corbetta (2004). Unseen, visually cued movements of the hands and feet (but not shifts of attention or the eyes) were found to increase EBA activity. This finding has been taken by others to show that EBA has a role in motor control and even to show that it is part of the human “mirror system.” In a subsequent replication, we (Peelen & Downing, 2005b) questioned the involvement of body-selective neurons in unseen hand movements: In our study, EBA only partially overlapped with the region activated by unseen hand movements, and MVPA in the overlap region showed no relationship between body and movement selectivity. In a response, Astafiev, Stanley, Shulman, and Corbetta (2005) showed that the overlap between EBA and the movement-related region depended on the control condition used: The overlap was substantial when contrasting hand and foot movements with a fixation baseline, but small when contrasting these movements with a matched control condition (covert detection without limb movements). Thus, the selective activation to body-part movements appears to be localized adjacent to EBA, at least when contrasted with a matched control condition. Nonetheless, the close proximity of these regions suggests a possible interaction between motor control and visual body processing.

Several authors have proposed that EBA has a motor role, in that its activity may be modulated by the output of the motor system. Specifically, it may receive an “efference copy” of motor commands in order to anticipate the perceptual consequences of

movement. For example, David et al. (2007; see also Yomogida et al., 2010) adopted such an account for an fMRI study in which participants controlled a simple visual cursor with unseen hand movements. On some trials, the visual feedback was manipulated so that it did not correspond to the participants' movements. EBA activity was greater on such trials, compared to when the feedback was correct. David et al. (2007) argued that EBA not only represents visual stimulation but also integrates visual and motor signals. Furthermore, David et al. (2009) used TMS combined with a similar protocol to show that stimulation of EBA increased response times on the detection of incorrect-feedback trials. Closer examination (described in detail in Kontaris, Wiggett, & Downing, 2009) suggests, however, that TMS stimulation may have also influenced performance on a motion task that was used as a control, and hence these results may have reflected disruption of adjacent hMT+. This possibility is relevant, given that the visual stimuli in these tasks were not body parts but simple visual cursors, and that hMT+ has itself been implicated in motor-visual mismatches (e.g., Whitney et al., 2007).

Kokal, Gazzola, and Keysers (2009) proposed that EBA is involved in integrating seen and performed joint actions in a different way—by coordinating one's own behavior with that of another individual (a review by Newman-Norlund, Noordzij, Meulenbroek, & Bekkering, 2007, makes a very similar proposal). In the key conditions of Kokal et al. (2009), the experimenter and the participant used finger movements in order to jointly create a specific angle on a clock-like device. This task produced more activity in lateral occipitotemporal cortex (EBA was not localized) than conditions in which either the participant or the experimenter alone moved the shared object. The authors argued from this finding that EBA has a role in “integrating observed and executed actions.” A simpler alternative account, however, is that observing two finger movements produces more activity in EBA (or nearby hMT+) than one finger movement.

To test the proposal that EBA and FBA receive feedback from the motor system about ongoing movements, Kontaris et al. (2009) showed participants movies of moving hands under varying conditions. In the “compatible” condition, the moving hand was a live on-screen view (via MR-compatible camera) of the participants' own movements. In the “incompatible” condition, the same stimuli were shown (having been recorded in previous blocks) while the participant made similar but incompatible hand movements. Regions receiving motor information about ongoing hand movements would be expected to respond differently in these conditions—for example, by showing a reduced response to

the expected, self-generated visual stimuli seen in the “compatible” condition. Consistent with this, activity in posterior superior temporal sulcus (pSTS) was suppressed to below-baseline levels by the participants' own movements in that condition (cf. Leube et al., 2003). In contrast, EBA and FBA responded strongly, but equally, to the compatible and incompatible conditions, and to a vision-only condition during which the same movies were shown without concurrent motor actions. This finding is not consistent with the idea that EBA or FBA receive an “efference copy” of motor commands or are otherwise involved in motor control.

Numerous studies have examined the brain areas involved in motor imitation, some of which have implicated EBA. For example, Jackson, Meltzoff, and Decety (2006) found extensive occipitotemporal activity for imitated versus passively observed movements, attributing this to EBA. Based on these findings (and the study by Astafiev et al., 2004), they argued that EBA automatically maps the actor's body parts on to those of an observed person, in order to support creation of an action plan. However, it seems very likely that imitation requires closer attention to the body stimuli than passive viewing, and that this explains the modulation. Indeed, Chaminade, Meltzoff, and Decety (2005) made just such an interpretation of a similar finding of modulation by imitation in occipitotemporal cortex. More recently, Molenberghs, Brander, Mattingley, and Cunnington (2010) have examined imitation of hand movements with stricter criteria, by identifying areas in which imitation produced greater activity than both passive viewing and action execution conditions. They found such activity only in pSTS.

Finally, motor imagery may produce activity in EBA and/or FBA. For example, Kuhn, Keizer, Rombouts, and Hommel (2011; see also Piefke et al., 2009) found that preparing to make either a limb movement or a face movement modulated EBA and FFA in the expected directions, even though these body parts were not in view. A difficulty of findings of this sort, however, is that they are consistent with multiple views of EBA/FBA functions: They could reflect involvement of these regions in the motor aspects of motor imagery, or simply visual imagery for the relevant body parts (see Blanke, Ionta, Fornari, Mohr, & Maeder, 2010). It is essentially the latter interpretation that Kuhn et al. (2011) adopt for their findings.

We find that the evidence does not support a direct role for EBA and FBA in the motor system. However, there is evidence in the studies reviewed above, and others, that occipitotemporal regions play some role in aspects of motor behavior. Activations are found in this region in response to both intransitive and transitive movements. Orlov et al. (2010) found small but

systematic biases across a wide swath of occipitotemporal cortex for visual depictions of different body parts, including but extending well beyond EBA and FBA. Most notably for present purposes, these biases also corresponded to similar biases in the same regions produced by unseen movements of the participants' own body parts. Furthermore, Oosterhof et al. (2010) found, using MVPA, that classifiers trained on the patterns of response in this general region (EBA was not localized) produced by different observed actions could discriminate among trials in which participants performed those movements out of view (and vice versa). This finding held for both intransitive and transitive actions, and suggests a crossmodal population coding of action in this general region.

Finally, recent evidence has identified a further occipitotemporal region that is relevant to the findings reviewed here. Bracci, Ietswaart, Peelen, and Cavina-Pratesi (2010) reported a hand-selective area that is adjacent to (and dissociable from) left EBA. This area responded selectively to images of hands, relative to feet and other human body parts. Given that they all used hand movements, many of the studies reviewed in this section, including those of Astafiev et al. (2004), Kontaris et al. (2009), Oosterhof et al. (2010), and Peelen and Downing (2005b), merit re-examination with localization of this hand-selective region.

EBA AND FBA CREATE COGNITIVELY UNELABORATED, PERCEPTUAL BODY REPRESENTATIONS

In sum, when stepping back for the broadest view, the above evidence can be characterized by two propositions: (1) EBA and FBA are involved in a wide range of perceptual tasks that involve some aspect of perceiving the human body or its parts; but (2) the evidence for these regions playing a high-level role that is specific to the representation of identity, emotion, body movement, or action, or in the control of motor behavior, is very limited.

We propose instead that the fMRI activations labeled “EBA” and “FBA” reflect relatively concentrated populations of neurons that respond selectively to the visual features that are highly typical of human bodies or body parts. These neurons jointly form a representation of perceived bodies and body parts, making this information available to other regions. They do this by extracting some (but only some) of the information about bodies that is implicit in “early” retinotopic visual representations and making it explicit. This process contributes importantly to

computations in other areas in which, for example, representations of emotions, actions, identity, body movements, and goals are extracted.

Coding of visual body/part features by neuronal activity patterns

A reasonable proposal is that this encoding of body information within EBA and FBA is carried out by changing patterns of activity across the neural populations local to these two areas. Taking that approach, we can make specific predictions about the representations formed in EBA and FBA (Figure 4). That is, what aspects of the body are highlighted and made explicit, and what aspects are left implicit?

First, we expect that the patterns of activity in these regions will vary systematically when exposed to different body parts (Op de Beeck, Brants, Baeck, & Wagemans, 2010) perhaps more so in EBA than FBA (Taylor et al., 2007). Likewise, the shape of the body and its parts will be explicitly represented in such a way that even relatively subtle differences in form will be amplified by the neural representation (relative, for example, to representations in earlier visual areas). Furthermore, we expect that the “space” of body shapes will be influenced by experience, so as to be skewed toward commonly experienced body types, sizes, and postures as well as views (Chan, Kravitz, Truong, Arizpe, & Baker, 2010).

Similar arguments can be made for posture—that is, systematically different activity patterns will map to the “space” of different possible postures that bodies can achieve. The coding for posture may be somewhat coarser than for form in light of findings such as those of Urgesi, Candidi et al. (2007). And, as we argued above, some postures may be “special” in that they represent “key frames” that are particularly useful for representing the positions of bodies and limbs efficiently. Note that some studies have examined the response to impossible body postures (Costantini et al., 2005; see also Avikainen, Liuhanen, Schurmann, & Hari, 2003; Cross, Mackie, Wolford, & Hamilton, 2010). We expect these will be coded with reference to the nearest possible posture, perhaps with an additional overall increase in activity due to attentional modulation (Candidi, Urgesi, Ionta, & Aglioti, 2008).

On the other hand, the neurons in EBA and FBA do not explicitly represent many high-level properties. For example, patterns of activity in these regions will relate to body shape rather than identity, so they will be more similar for two bodies or body parts with highly similar shape (even across different viewing conditions such as occlusion, viewpoint, etc.; Taylor et al., 2010) than for

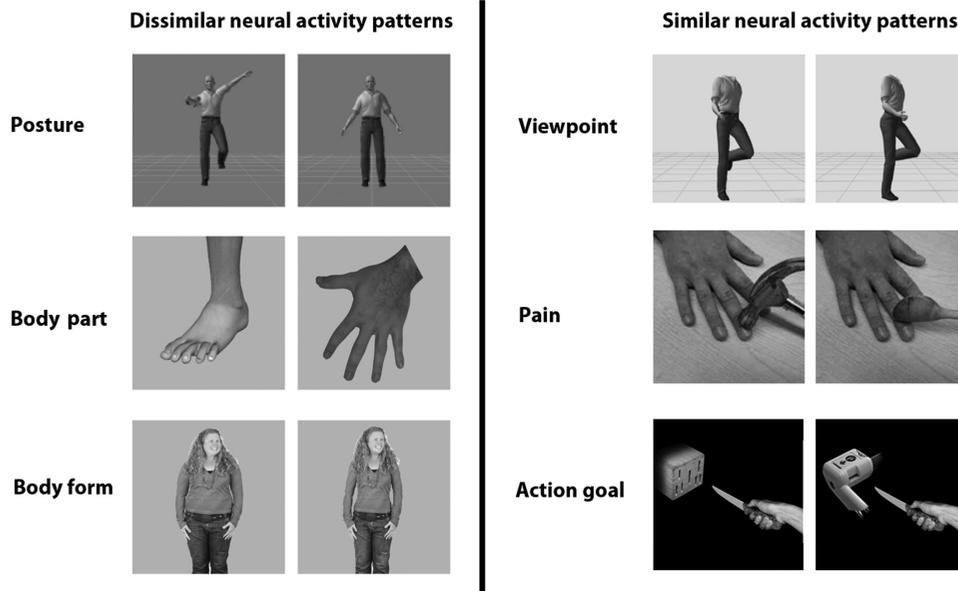


Figure 4. The present framework predicts that, in the extrastriate and fusiform body areas, distinct patterns of activity across neural populations make explicit some aspects of the visual appearance of human bodies but not others. The left panel illustrates the prediction that (other factors being equal), different patterns of neural activity in EBA and FBA will be elicited by seeing the same body holding different postures; different body parts; and different body shapes, sizes, and forms. In contrast, the right panel illustrates the prediction that (other factors being equal), similar patterns of neural activity in EBA and FBA will be elicited by varying viewpoints of the same body (up to some tolerance); the same body part in different emotion/pain contexts; and the same body part undertaking to achieve different goals. Right-side figures adapted from Taylor, Wiggett, and Downing (2010); Morrison et al. (2007); and Bach et al. (2010), respectively.

two images of the same person where shape has changed (e.g., due to weight gain or age), or for two different body parts of the same person. Likewise, where the same body or body part was seen to be moving in different ways, or engaging in different interactions with the same object, neural activity patterns would remain highly similar (assuming other factors were constant). And, again, a similar argument would be made for the case of motor control—the same body stimuli seen in the context of different ongoing motor behavior by the observer would produce similar patterns of activity.

This consideration of patterns of neural activity suggests that neural populations in EBA and FBA are not monolithic but rather may have a complex structure. The most recent evidence has begun to support this idea. For example, as noted above, Bracci et al. (2010) reported a hand-selective region that falls near, but can be dissociated from, EBA; and op de Beek et al. (2010) identified distinct foci that respond maximally to torsos and to hands. Likewise, Weiner and Grill-Spector (2011) showed evidence for discrete subregions of EBA that fall in a consistent anatomical relationship to hMT+ and retinotopic regions. In the fusiform gyrus, Michels et al. (2009) identified separable subregions that respond differentially to point-light “walker” stimuli depending on the direction in which they are seen to walk. These findings may

generally be seen as extensions of the idea of “EBA” or “FBA” that we have developed. That is, they shed light on the local structure of the body representations in these regions, but they do not suggest an entirely different functional role for them.

Local anatomical context

As we and others have discussed (Minnebusch & Daum, 2009; Peelen & Downing, 2007a; Slaughter & Heron, 2004; Taylor et al., 2007), there may be useful parallels to be drawn between the cortical representations of bodies and of other stimulus kinds. The model we develop here can be readily compared, for example, to the structural encoding component of Bruce and Young’s (1986) model of face perception, in which the visual properties of faces are extracted and made available to other systems for the analysis of properties such as identification and emotion recognition. This comparison may indeed be more than just an analogy. Bodies and faces, of course, are commonly perceived together, and the close overlap of FFA and FBA hints at functional interactions. Such interactions are further suggested by recent findings of cross-adaptation between faces and bodies (Ghuman, McDaniel, & Martin, 2010) and the discovery that behavioral costs of body inversion depend on the presence of

the head (Minnebusch, Suchan, & Daum, 2009; Yovel, Pelc, & Lubetzky, 2010) and relate to activity in face-selective areas (Brandman & Yovel, 2010).

More broadly, a similar gross, neuroanatomical structure is seen in occipitotemporal cortex responses to bodies, faces, and objects: The occipital face area (Gauthier et al., 2000; Puce et al., 1996; Rossion et al., 2003) and the LO subregion (Grill-Spector et al., 1999) of the object-selective lateral occipital complex (LOC) (Malach et al., 1995) are found near EBA. Similarly, FFA and the pFs subregion of LOC are found near FBA. As noted above, EBA forms a body representation that is more part-based than FBA. Similar distinctions are found for faces (stronger representation of parts in OFA than FFA; e.g., Liu, Harris, & Kanwisher, 2010) and for objects (LO vs. pFs; e.g., Drucker & Aguirre, 2009). These parallels and others (e.g., Schwarzlose, Swisher, Dang, & Kanwisher, 2008) suggest there is a domain-general division of labor between lateral and ventral occipitotemporal extrastriate areas. This proposal (and an extensive review of the relevant evidence) is considered in depth elsewhere (Taylor & Downing, 2011).

Recent evidence for broad, diffuse body representations in occipitotemporal cortex may seem at odds with a focus on selective regions such as EBA and FBA. Orlov et al. (2010) found a widespread mosaic of broad regions that respond in subtle but systematic ways to perceiving and moving different body parts (e.g., to upper limbs vs. torsos). These responses encompass (but extend well beyond) EBA and FBA, and these findings suggest that some aspects of the perception (and even movement) of body parts could be represented in a distributed way across this broad cortical territory. These findings do not necessarily challenge the importance of focal, selective regions such as those we examine here. Rather they emphasize that aspects of body perception may extend further than previously thought. There may be multiple representations of bodies (and other stimuli) that coexist at different spatial scales in these areas (cf. Graziano & Aflalo, 2007). Indeed, positing a broad, diffuse occipitotemporal representation of bodies, surrounding local “peaks,” may help to account for the familial relationship among many of the distinct but neighboring focal activations discussed here, such as those responding to bodies, faces, tools, action, visual motion, hands, and the like.

Global connections

It is a truism of cognitive neuroscience that task performance is supported by the activity of neural networks. Often, unfortunately, the term “network” is used loosely to describe brain regions that are coactivated in fMRI by

the same contrast, in the absence of significant direct evidence for connectivity (e.g., Wiggett & Downing, 2008). Although recent studies address this gap in domains such as face processing, using such tools as dynamic causal modeling (e.g., Fairhall et al., 2007), to our knowledge, there is no extant evidence that pertains to extrastriate body-selective regions.

Nonetheless, it is an entirely reasonable hypothesis that the perceptual information extracted in EBA and FBA is made available by functional connections to other regions. It is the integration of this information with that computed in other regions that together will explain body perception in its fullness. A key question that is at stake when discussing such a putative functional network is to what extent the representations in a given area are penetrated or shaped by those in other regions. What are the limits of the influence of the activity in other areas on the activity in EBA and FBA? The space of possibilities ranges between two extremes. On the one hand, these regions could be entirely encapsulated in the sense that they strictly analyze the lower-level visual signals they receive, and the result is passed on to other brain areas without any further influence by the computations made in those areas. On the other hand, it could be that among the “network” of areas that concerns itself with the perception (and indeed movement) of bodies, the range of functions is widely distributed, and the relatively greater response in one area to visual stimuli and another to motor behavior is a difference of degree rather than kind. On this view, in the extreme it makes little sense at all to consider EBA (or FBA) in isolation, as its functions can only be understood in the context of the entire network.

Our speculation is that the truth leans closer to the former picture than the latter. There are good functional arguments for why the perceptual functions of a network should not be fully penetrable by the operations of other brain areas; a relatively stimulus-bound, veridical representation can be important, for example, when expectations are violated. An important exception to this principle is that the representations in body-selective brain areas (and other extrastriate areas) will be strongly modulated by the focus of attention. This may occur indirectly, such as by spatial attention mechanisms affecting retinotopic maps, with the knock-on effect of modulating body representations according to the contents of attended locations (cf. Downing, Liu, & Kanwisher, 2001). Additionally, attention may directly modulate activity in body-selective regions as a way of supporting a template in the service of an abstractly specified task (Peelen et al., 2009). Given some of the considerations above about substructure, we may further

suppose that attentional effects can be general—across whole body-selective areas—or target specific limbs, say, where those are most relevant.

On our account, a body-selective neuron in EBA or FBA does not “know” (for example) whether someone is angry or sad—it does not contain “angry body detectors.” There is no systematic mapping between the patterns of neural activity in these regions, on the one hand, and the body postures related to different emotions, on the other hand. Other regions interpret the emotion of seen bodies, on the basis of the information provided by EBA and FBA as well as other areas that represent semantic knowledge, scene context, and the like. One result of this process may be attentional feedback to occipitotemporal cortex. If the hands, for example, are important for expressing emotions, then attention will tend to select the hands in the image when emotion is relevant. Hand-related activity patterns in the body-selective areas will be enhanced accordingly. In this way, attention modulates the responses of body-selective neurons to ensure that resources are allocated efficiently to process behaviorally relevant input.

Puzzles

We have focused on vision, but some new evidence points to occipitotemporal body representations in other modalities. Kitada, Johnsrude, Kochiyama, and Lederman (2009) found separate subclusters in the lateral occipitotemporal cortex that respond selectively to either visually or haptically presented body parts. More recently, Costantini et al. (2011) found evidence for right (but not left) EBA engagement by haptic aspects of body-part perception (compared to non-body objects). When considered alongside studies of object recognition that show an overlap between tactile and visual representations (Amedi, von Kriegstein, Van Atteveldt, Beauchamp, & Naumer, 2005), and “typical” occipitotemporal patterns of selectivity in blind participants for objects (Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Pietrini et al., 2004) and actions (Ricciardi et al., 2009), these findings point to nonvisual influences on the functional organization of the extrastriate cortex. With respect to the present discussion of EBA and FBA, however, we predict that where tactile stimulation engages these regions, it will be in the service of similar functional properties to those discussed here for the domain of vision.

Some further puzzles remain in the poorly understood influences of nonsensory factors on the characteristics of EBA and FBA. For example, the handedness of participants is related to the lateralization of EBA (but

not hMT+) and FFA, such that right-handers, but not left-handers, show a right-hemisphere bias in the size of these selective regions (Willems, Peelen, & Hagoort, 2010). In parallel, it appears that women show a stronger right-lateralization of EBA and FBA than men (in a study in which all but one of the participants were right-handers; Aleong & Paus, 2010). This may relate to left-visual-field specific body size estimation deficits found in women but not men (Mohr, Porter, & Benton, 2007). The present framework does not account for these (possibly interacting) effects of handedness, gender, and hemisphere.

CONCLUSION

We have sought to take a deliberately simple account of occipitotemporal body representations as far as possible, and, in doing so, to flush out gaps in our knowledge and to provoke debate. This simple model succeeds well in accounting for extant data. Many findings that appear to show elaborated body or person representations in EBA or FBA can be explained with an appeal to simpler principles such as the influence of attention. We argue that body-selective regions exist because of the important and complex information that body parts convey. The fMRI activations that we label “EBA” and “FBA” reflect the activity of neurons that analyze the form and configuration of bodies in a highly efficient and specialized manner. This information is then made available to other brain areas that extract and make explicit the meaningful signals that are implicit in the visual appearance of the body. The joint activity of these regions is what constitutes understanding of an image; but, we argue, the influence of activity in other regions on EBA and FBA is largely limited to attentional modulation.

This discussion helps to highlight some of the many challenges for future research. In our view, these include the following: discovering the detailed structure of body representations in EBA and FBA and how they may differ from each other; investigating their similarities and differences to anatomically aligned object and face representations; obtaining further evidence on the nonvisual influences on activity in these regions; understanding how they relate to diffuse patterns of visual and motor body-related information distributed throughout occipitotemporal cortex; and testing explicitly the proposal that these regions form functional connections with other brain areas in order to jointly create coherent, contextualized, and useful representations of the body.

Commentaries

Do body-part concepts depend on the EBA/FBA?

David Kemmerer^{1,2,3}

¹Department of Speech, Language, and Hearing Sciences, Purdue University, West Lafayette, IN, USA

²Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA

³Department of Neurology, Division of Cognitive Neuroscience, University of Iowa College of Medicine, Iowa City, IA, USA

E-mail: kemmerer@purdue.edu

<http://dx.doi.org/10.1080/17588928.2011.604718>

Abstract: Downing and Peelen argue that the EBA/FBA represent body-part shapes in a highly schematic manner that is independent of personal identity, emotional expression, movement pattern, and action goal, and that cuts across visual and haptic modalities. According to the grounded cognition framework, these properties make the EBA/FBA suitable for processing body-part shapes not only for perceptual purposes but also for conceptual purposes. Any account of the neural substrates of body-part concepts must, however, accommodate significant cross-linguistic diversity in this semantic domain. Hence, an alternative possibility is that the shape components of body-part concepts depend on areas adjacent to the EBA/FBA.

A prominent theory of conceptual knowledge is the grounded cognition framework, which maintains that concepts are not completely divorced from modality-specific systems for perception and action, but instead overlap with them to some degree (Barsalou, 2008; Kiefer & Pulvermüller, 2011; Martin, 2007). Consider, for example, an fMRI study by Chao, Haxby, and Martin (1999) that focused on the perceptual and conceptual processing of animals and tools. Perceptual processing was probed with passive viewing tasks and match-to-sample tasks, and conceptual processing was probed with picture-naming tasks and property-verification tasks. Across all of the tasks, perceptual as well as conceptual, greater activation

for animals was found in a lateral portion of the mid-fusiform gyrus, whereas greater activation for tools was found in a medial portion of the mid-fusiform gyrus. These regions probably represent the shapes of animals and tools, and the fact that they were activated not only by pictures, but also by words, supports the grounded cognition framework. Moreover, several other studies have generated convergent results which suggest that the word-induced fusiform activations reflect the retrieval of shape properties for conceptual purposes, and are not due to mere “imagery” (Martin, 2007).

Although much has been learned about the neural substrates of the shape properties of animal and tool concepts, almost nothing is known about the neural substrates of the shape properties of body-part concepts, as expressed by terms like *arm*, *hand*, *leg*, and *foot*. This gap in the literature is surprising, given the tremendous interest in body representation that has recently emerged. There is some neuropsychological evidence that body-part concepts depend on the lateral/ventral occipitotemporal cortices, among other regions (Kemmerer & Tranel, 2008). To my knowledge, however, no studies have tested the hypothesis, derived from the strongest form of the grounded cognition framework, that the shape properties of body-part concepts rely specifically on the EBA/FBA or on neighboring areas that also seem to contribute to body-part perception.

According to Downing and Peelen, the EBA/FBA are tuned to the domain of body-part shapes in several ways: They capture “bare bones” schematizations of these objects, as shown by their sensitivity to silhouettes, cartoons, and stick figures; they respond to body-part shapes regardless of personal identity, emotional expression, movement pattern, and action goal; and they generalize across visual and haptic modalities. Interestingly, these representational capacities appear to make the EBA/FBA well suited to processing body-part shapes for both perceptual and conceptual purposes. Hence, an advocate of the grounded cognition framework might predict that understanding a word like *leg* involves activating the same patches of the EBA/FBA, or the same population codes in these regions, that are engaged during the perceptual recognition of legs.

It is noteworthy, however, that although most languages have words that segment the body according to salient perceptual discontinuities, there is still substantial variation. To take a few examples, Savosavo has a single category for leg that begins at the hip joint and encompasses the foot, ignoring both knee and ankle discontinuities; Yéfi Dnye has one term for the upper leg and another term for the lower leg plus the foot, thus respecting the knee discontinuity but ignoring the ankle discontinuity; Jahai recognizes all three parts—upper leg, lower leg, and foot; and Tidore has one term that covers the foot, lower leg, and lower part of the thigh, and a separate term for “groin” that includes the upper part of the thigh, thus making a category distinction in the absence of a corporeal discontinuity (Majid, 2010).

Any account of the neural underpinnings of body-part concepts must accommodate this diversity. Perhaps language is one of the experiential/cultural factors that, according to Downing and Peelen, influences the EBA/FBA. Alternatively, there may be multiple occipitotemporal body-part maps, and the shape properties of body-part concepts may be subserved by areas near the EBA/FBA. In this situation, the relationships between perceptual and conceptual body-part representations would probably be looser, but they would still be quite close, consistent with a weaker form of the grounded cognition framework. The key point is that both of these possibilities, and others, are ripe for investigation.

* * *

Adaptation studies suggest interactive feedback shapes responses in occipitotemporal regions

Michael P. Ewbank

MRC Cognition and Brain Sciences Unit,
Cambridge, UK

E-mail: michael.ewbank@mrc-cbu.cam.ac.uk

<http://dx.doi.org/10.1080/17588928.2011.604719>

Abstract: Downing and Peelen portray the EBA and FBA as a largely impenetrable system, passing on visual signals to other cortical areas where high-level information is extracted.

They suggest that the influence of other regions on EBA and FBA is primarily limited to changes in attentional modulation. In the following commentary, this proposal is evaluated within the context of a predictive coding framework. Recent evidence is discussed indicating that fMRI-adaptation effects in occipitotemporal cortex, including EBA and FBA, are consistent with the influence of higher-level modulation, suggesting that responses in these regions are shaped through the interactive feedback of a hierarchical network.

In their discussion paper, Downing and Peelen propose that the joint activity of the extrastriate body area (EBA) and the fusiform body area (FBA) creates a detailed representation of the visual appearance of the human body. They also suggest that the perceptual functions of these regions are largely impenetrable by the operations of other brain areas. By their own admission, the authors present an oversimplified account of body representations in the occipitotemporal cortex. However, a simple model need not characterize EBA and FBA as cognitively impenetrable modules; instead, findings from fMRI-adaptation studies suggest that responses in these regions can be shaped through interactive feedback.

Recently, we measured fMRI-adaptation in EBA and FBA to presentations of the same body compared to different bodies (Ewbank et al., 2011). Both regions showed adaptation to bodies that was invariant to substantial changes in size and view. One interpretation of this finding is that both EBA and FBA hold a relatively high-level representation of body identity. However, using dynamic causal modeling, we were able to demonstrate that adaptation is associated with a change in effective connectivity from FBA to EBA, indicating that adaptation in EBA—across changes in size and view—is the consequence of modulation from FBA. Our findings thus provide direct evidence that top-down modulation may underlie visual adaptation within the occipitotemporal cortex. Moreover, other evidence suggests that such occipitotemporal adaptation effects can be modulated by top-down input from other “systems.” For example, Summerfield et al. (2008) found greater adaptation to faces in the fusiform face area (FFA) when repetitions were expected, reflecting top-down influences from the prefrontal cortex.

These effects are consistent with models of predictive coding in which adaptation is thought to reflect a decrease in prediction error between bottom-up (stimulus-related) and top-down (prediction-related) inputs (Friston, 2005;

Henson, 2003). Indeed, in a previous study, Downing and colleagues themselves suggested that adaptation in EBA and FBA may reflect higher-level modulation (Taylor, Wiggett, & Downing, 2010). Here, they found that the presentation of scrambled masks disrupted adaptation to images of the same body across view, and suggested that this effect may reflect an interruption of the later stages of neural activity in EBA and FBA, “which may be influenced by reciprocal interactions with higher level cortical areas.” ERP evidence also indicates that adaptation across view occurs in a later time period than adaptation to identical images of objects (Schendan & Kutas, 2003). These results suggest that top-down influences on EBA and FBA are unlikely to be restricted to attentional modulation.

In the current paper, the authors propose that a “stimulus-bound” representation in EBA and FBA “may be important for determining when expectations are violated.” This suggests neurons in these regions respond monotonically to all input (unless modulated by changes in attention and other factors). The advantage of a hierarchical model, however, is that it enables the brain to construct prior expectations in a dynamic fashion—rather than being stimulus bound, energy-costly signals are focused on rare inputs, alerting the system to important changes. Thus, neurons in EBA and FBA are suppressed when the same body is expected (e.g., during repetition)—including transitions in size and view—but remain sensitive to unpredicted transitions, such as random changes in body shape (Aleong & Paus, 2010). Similarly, EBA and FBA show an increased response to contorted compared to normal body postures (Cross, Mackie, Wolford, & Hamilton, 2010) and incoherent compared to coherent action sequences (Downing, Peelen, Wiggett, & Tew, 2006).

The key aspect of predictive coding models is that each level in a hierarchy is penetrable by predictions received from the level above. The FBA is unlikely to correspond to the highest stage of body processing, and therefore responses in this region are also likely to be modulated by inferences in higher-level areas. Within this framework, adaptation to repetition of the same body is the consequence of interactions between regions rather than being localized to an individual area.

It appears likely that EBA and FBA extract visual information that contributes to computations pertaining to identity. However, adaptation studies suggest that the relationship between EBA and FBA, and the relationship between these regions and higher-level areas, is likely to

be reciprocal, with activity in higher-level areas dynamically shaping responsivity in lower-levels regions.

* * *

Human body perception and higher-level person perception are dissociated in early development

Virginia Slaughter

Early Cognitive Development Centre, School of Psychology, University of Queensland, Brisbane, Australia

E-mail: vps@psy.uq.edu.au

<http://dx.doi.org/10.1080/17588928.2011.604720>

Abstract: Developmental data support the proposal that human body perceptual processing is distinct from other aspects of person perception. Infants are sensitive to human bodily motion and attribute goals to human arm movements before they demonstrate recognition of human body structure. The developmental data suggest the possibility of bidirectional linkages between EBA- and FBA-mediated representations and these higher-level elements of person perception.

Downing and Peelen’s conclusion that EBA and FBA encode structural details of the human body and its parts, but do not directly contribute to higher-level person perception, is consistent with developmental work on these topics. Behavioral research with human infants reveals dissociations between body perception and many of the other capacities discussed by Downing and Peelen. I will focus on two of them: recognition of human motion patterns and detection of goal-directed human movement.

The available evidence indicates that EBA and FBA play a causal role in adults’ visual perception of the human body. This is evident in differential responsiveness of these regions to intact human body images as compared to scrambled bodies or other objects. In our behavioral studies with infants, we evaluate visual discrimination of intact human bodies from scrambled non-bodies constructed by moving the arms and legs from their canonical locations. This task indicates that reliable recognition of human body structure does not

emerge until the end of the first year of life (Heron & Slaughter, 2010). We have speculated that this is because, prior to 9–12 months, infants have little visual access to whole bodies; they regularly see other people's faces, their own and others' hands (Aslin, 2009), and their own legs. But they may not have much visual experience of how these parts fit together. So prior to the end of the first year of life, infants do not appear to have access to detailed structural representations of the human body.

By contrast, perception and recognition of human body movement emerges within the first few months of life. Behavioral studies indicate discrimination of intact versus phase-shifted human point light display (PLD) walkers by 3 months of age and discrimination of upright from inverted PLD walkers by 5 months (see Bertenthal, 1993). Recent ERP experiments with 8-month-olds revealed different patterns of parietal activation while infants view normal versus scrambled human PLD walkers (Hirai & Hiraki, 2005) as well as upright versus inverted ones (Reid, Hoehl, & Striano, 2006). Therefore, perception of whole-body human movement patterns is an earlier achievement than perception of human body structure.

Attributing goals to human movement is also developmentally distinct from body perception. By 6 months of age, infants encode the goal of a moving human arm (Kiraly, Jovanovic, Prinz, Aschersleben, & Gergely, 2003). That is, when they view an arm reaching for one of two objects, infants expect the arm's next reach to go for the same object, consistent with its prior goal. Little is currently known about infants' perception of individual, salient body parts. However, a recent study revealed that 6-month-olds attribute goals to human movement even when it involves a violation of body structure (e.g., when the arm moving to grasp an object bends impossibly) (Southgate, Johnson, & Csibra, 2008). So goal attribution to human reaching movements emerges prior to whole-body recognition, and also appears to be distinct from expectations about how arms themselves should appear.

Downing and Peelen favor a model in which EBA- and FBA-mediated structural representations of the body are functionally encapsulated from higher-level inferential systems. They imply that perceptual information computed by body-selective areas constitute representational primitives that are then passed "upward" for more complex processing. This is a logical model that may well describe what occurs in the adult brain. However, as described above, some aspects of higher-level processing (e.g., of human

body movement and goal-directed actions) are evident before infants exhibit knowledge about human body structure. This means that at least some aspects of higher-level person perception can occur without the kind of information computed by EBA and FBA. It also suggests that body structural representations may be derived from (rather than be a precursor to) those higher-level processes, or that there may be bidirectional linkages, at least early in development.

* * *

No two are the same: Body shape *is* part of identifying others

Richard Ramsey^{1,2}, Hein T. van Schie³, and Emily S. Cross^{2,3}

¹Faculté de Psychologie et des Sciences de l'Éducation, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

²Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, Gwynedd, UK

³Behavioural Science Institute, Radboud University, Nijmegen, The Netherlands

E-mail: richard.ramsey@uclouvain.be

<http://dx.doi.org/10.1080/17588928.2011.604721>

Abstract: Downing and Peelen argue for a clear distinction between body and identity representation, with the former performed by EBA and FBA, and the latter performed elsewhere in the brain. Under a predictive coding account, we argue that this separation is unnecessary: Representing bodies is part of representing identity. While neurons in EBA and FBA may only code for body shape and posture, we propose that they are a part of a reciprocally connected cortical network that functions to minimize prediction error when making identity inferences. We propose a novel way to test the hypothesis that EBA and FBA are critically involved in person identification.

Downing & Peelen offer a "cognitively unelaborate" interpretation of research examining EBA and FBA. The authors argue that "the role of these regions [EBA and FBA] consists in creating a perceptual representation of the shape and posture of the body and its parts, which may then be used by other brain regions (e.g., the anterior temporal lobes; Kriegeskorte et al., 2007) to represent person identity explicitly" (p. 193).

Such a proposal assumes that the coding of physical features is separate from a process that determines identity. However, the authors allow for exchange between these distinct processes (and brain regions). For example, “Note that our account does not exclude the possibility that responses in EBA and FBA can be influenced by identity through top-down modulation: The sight of a romantic partner (or, indeed, the self) may increase responses in EBA/FBA due to increases in attention and arousal” (p. 193). Under this framework, it appears that body processing in extrastriate cortex is *not* part of a “who” system involved in person identification (Georgieff & Jeannerod, 1998), but rather supplies input to it by passing on body shape and postural information. This implies that body shape and posture are not part of “higher-level” identity processes. Rather, EBA and FBA neurons code physical features in an agent-blind manner; that is, they do not contribute to differentiating between identities.

While we agree that current evidence does not support an interpretation beyond coding of physical features, we propose that EBA and FBA *do* play a critical role in understanding identity by being part of a network of reciprocally connected neural regions that “bias” the neural signals involved in making identity inferences. To illustrate this point, we revisit the “romantic partner” example (p. 193). When a romantic partner walks into a room, coding of her physical features in EBA and FBA, such as a small head and skinny arms, would bias a “who” system toward supporting an inference about the person being a romantic partner, rather than a different acquaintance (with a distinct body shape). This biasing process is similar to the predictive coding account of action perception, which hypothesizes that the brain relies upon Bayesian models to predict how an action should unfold across time, based on prior experience (Kilner, Friston, & Frith, 2007). Perceiving a body shape that matches your romantic partner’s does not mean it is *definitely* your romantic partner, but based on your prior experience with the perceived body shape, it is statistically more likely to be your partner than another person. In other words, while neurons in EBA and FBA may code only body shape and posture, in doing so they contribute to reducing prediction error throughout a reciprocally connected network of brain regions, which together determine one’s current identity inference. Importantly, EBA and FBA generate only part of the biasing signal that contributes to making an identity

inference; one must link this signal with additional biasing signals that relate to other prior person experiences, such as accent, gait, clothes, hairstyle, etc., and this, we agree, likely occurs elsewhere in this cortical network, beyond EBA and FBA.

To test whether EBA and FBA are involved in identifying “who” somebody is according to a predictive coding framework, we suggest that standard neuroimaging experiments lack the sensitivity to address this issue (e.g., Hodzic, Muckli, Singer, & Stirn, 2009); instead, we advocate the use of causality mapping techniques, such as dynamic causal modeling and Granger causality mapping. In a neuroimaging experiment where participants must identify familiar and unfamiliar bodies, causality mapping would enable the flow of information processing to be traced from occipitotemporal areas to anterior regions (e.g., anterior temporal lobes), and the inverse direction. If EBA and FBA do indeed play a role in identifying “who” somebody is, differential directional flow between these regions should emerge when identifying familiar versus unfamiliar bodies. For example, in perceiving familiar individuals, there may be more information flow “backward” from anterior to posterior brain regions, reflecting a top-down biasing signal based on prior information about the person. In contrast, in perceiving unfamiliar individuals, there may be more information flow “forward” from posterior to anterior brain regions, reflecting more bottom-up processing of body shape and posture.

In summary, Downing and Peelen imply that body shape and posture are coded independently of identity, as identity only involves what the authors label as “higher-level processes.” Whether they are labeled high- or low-level, we argue that unique features of a person’s body contribute to knowing who a person is. Moreover, we suggest that EBA and FBA are part of a cortical network of brain areas that rely upon Bayesian models to predict likely identity from prior person experience. As such, we argue that EBA and FBA are integral nodes of a “who” system for making identity inferences. We suggest that a worthwhile pursuit at this stage would be to employ more sensitive neuroimaging measures to determine whether EBA and FBA might assist with body identification according to a Bayesian framework of predictive coding.

* * *

When perception and attention collide: Neural processing in EBA and FBA

Susanne Quadflieg and Bruno Rossion

Department of Psychology, Catholic University of Louvain, Louvain-La-Neuve, Belgium
E-mail: susanne.quadflieg@uclouvain.be

<http://dx.doi.org/10.1080/17588928.2011.604722>

Abstract: In their timely review, Downing and Peelen differentiate between neural systems dedicated to body perception and body-based person inferences. Rather than supporting their view of these operations as largely separate mental and neural entities, we emphasize reasons to favor a stronger notion of co-dependency.

Based on their discussion of research findings concerning the extrastriate body area (EBA) and the fusiform body area (FBA), the authors conclude that these regions provide a “cognitively unelaborated perceptual framework [of bodies] that allows other cortical systems to exploit the rich, socially relevant information.” In so doing, the authors iterate the idea of distinguishing between a core neural system of person perception and an extended system of person inferences as originally introduced by Haxby, Hoffman, and Gobbini (2000) in the realm of face processing. According to this approach, one set of brain regions analyzes the visual appearance of people, whereas additional sites subsequently use this information to generate person inferences (e.g., regarding a target’s identity, see Macrae & Quadflieg, 2010).

An extensive body of work indicates, however, that connectivity between brain regions is usually bidirectional and that information reaching a specific cortical site tends to be processed under the influence of cross-regional interactions (e.g., Friston, 2005). From a computational point of view, it also seems unlikely that feed-forward mechanisms alone can accomplish the rapid and adequate recognition of complex visual input (e.g., Mumford, 1992). Hence, it has been argued that perceptual processes are habitually penetrated and disambiguated by higher-level cognitive factors such as a perceiver’s expectations and processing goals (Bar, 2009; Bruner, 1973).

To counter such a view in the realm of body perception, Downing and Peelen emphasize that regions such as the EBA and FBA achieve “relatively stimulus-bound” representations that are “not fully penetrable by the operations of other brain areas” (p. 202). Alas, the authors own choice of words gives away the caveat. How *relatively* stimulus-bound are the representations and to what extent (if not *fully*) are they modifiable? Importantly, accepting the idea of penetration does not result in the assumption that EBA and FBA themselves compute higher-order cognitive inferences—in which case, there would be no necessity for penetration. Rather, the assumption of penetration argues that due to operations in other brain sites, processes unfolding in the target region are modified.

To illustrate this idea, consider the following results (Quadflieg et al., 2011): Perceivers asked to sex-categorize men and women portrayed in various types of occupational clothing displayed enhanced activity in EBA and FBA when a target’s attire violated common gender stereotypes (e.g., when seeing a female firefighter). These data seem incompatible with Downing and Peelen’s claim that core body-perception areas create cognitively unelaborated representations. Of course, EBA and FBA are not argued to “know” whether a target fits cultural stereotypes. Nevertheless, the finding indicates that “higher-order” expectations can help or hinder building a coherent person percept.

Note that changes in EBA and FBA activation across experimental conditions as illustrated here may reflect mere attentional modulations during stimulus processing. According to Downing and Peelen, such modulations may be caused by sampling differences (i.e., differences in preferentially attended-to contents) or template differences (i.e., differences in body templates used in the service of task completion). Intriguingly, both mechanisms are also listed by the authors to characterize the type of perceptual processing occurring in core body-perception regions. Populations of neurons in EBA and FBA are argued to extract and bind body information in a non-exhaustive manner (only *some* of the information) and based on templates “useful for representing the positions of bodies and limbs” (p. 200). This observation then raises the question of how attention-related modulations actually differ from “perceptual” modulations if both comprise the selective sampling, binding, and template-based encoding of body information.

In our view, an empirically falsifiable differentiation between perceptual and attentional modulations forms a necessary prerequisite for understanding aspects of penetration in body perception. This lofty goal cannot be addressed by fMRI alone. Rather, dissecting the exact temporal unfolding of body processing across brain regions through high-density recordings of EEG/MEG in humans (e.g., Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006), or through direct recordings of single-cell responses in nonhuman primates (e.g., Pinsk et al., 2009), is likely to help with such a feat. Alternatively, investigating whether receptive field properties of neurons located in EBA and FBA vary depending on expectations and task demands (see David, Hayden, Mazer, & Gallant, 2008) will add to our understanding of whether it is person perception that solely informs person inferences, or whether person inferences also shape person perception.

* * *

Differential contributions of occipitotemporal regions to person perception

Annie W.-Y. Chan and Chris I. Baker

Laboratory of Brain and Cognition, National Institute of Mental Health, NIH, Bethesda, MD, USA
E-mail: chanannie@mail.nih.gov

<http://dx.doi.org/10.1080/17588928.2011.604723>

Abstract: Downing and Peelen have produced an excellent review synthesizing the current literature on the processing of body stimuli in visual cortex. However, while they consider the extrastriate body area (EBA) and fusiform body area (FBA) together, these regions are physically separate in cortex and likely contribute differentially to person perception. Here, we evaluate the hierarchical view of processing in EBA and FBA and highlight the visual field biases in these regions, which may provide insight into their origin and functional roles.

We agree with Downing and Peelen that representations in EBA and FBA primarily reflect visual features of bodies, not higher-level cognitive information such as identity or emotion. However, there are two critical aspects of these regions that remain unclear; namely,

why are there two regions and what are the differential contributions of EBA and FBA to person perception?

Are EBA and FBA hierarchical?

Downing and colleagues have proposed that EBA primarily represents individual body parts whereas FBA represents the whole body (combination of body parts). Support for this view comes primarily from a study (Taylor, Wiggett, & Downing, 2007) demonstrating that, while the selectivity in EBA increased gradually with increasing amounts of the body presented (finger, hand, limb, whole body), FBA exhibited a step-like function with no selectivity for single fingers or hands. Such a hierarchical account is similar to that proposed for faces and objects, for which there are also two selective regions, one lateral and one ventral (e.g., Liu, Harris, & Kanwisher, 2010). However, as pointed out elsewhere (Op de Beeck, Brants, Baeck, & Wagemans, 2010), Taylor and colleagues did not counterbalance the body stimuli such that each body part occurred in both isolated and combined conditions. Thus, for example, torsos only ever occurred in combination with fingers, hands, and arms, and apparent selectivity for combinations of body parts could be confused with torso selectivity, which has been reported near FBA (Op de Beeck et al., 2010; Orlov, Makin, & Zohary, 2010). Further, other studies have found no difference in selectivity in FBA for isolated, mixed body parts compared with headless bodies (Schwarzlose, Baker, & Kanwisher, 2005). Thus, the current evidence for hierarchical processing within body selective regions is not entirely compelling.

What do visual field biases tell us about EBA and FBA?

Both EBA and FBA show spatial biases within the visual field, and this may be important for understanding their roles in person perception. First, FBA lies in a region of cortex with a foveal bias (Levy, Hasson, Avidan, Hendler, & Malach, 2001) and exhibits stronger responses to foveal than peripheral stimuli (Schwarzlose, Swisher, Dang, & Kanwisher, 2008). In contrast, EBA shows stronger responses for peripheral than foveal stimuli (Schwarzlose et al., 2008), and much of EBA appears to overlap regions with an underlying preference for peripheral space (Weiner &

Grill-Spector, 2011). Thus, while FBA appears to be foveally biased, EBA appears to have a bias for more peripheral parts of the visual field.

Second, EBA shows an elevation bias with stronger responses for lower compared to upper visual field body stimuli (Schwarzlose et al., 2008), and much of EBA overlaps maps of the lower visual field (Weiner & Grill-Spector, 2011). This lower-field bias is also observed in nearby regions selective for motion (middle temporal area, MT; Maunsell & Van Essen, 1987) and objects (Kravitz, Kriegeskorte, & Baker, 2010), and is consistent with their relative proximity to the lower field representation in early visual cortex. In contrast, FBA does not show a clear bias to either the upper or the lower visual field (Schwarzlose et al., 2008), perhaps because of the strong foveal bias, although an upper-field bias has been reported in nearby regions of ventral occipitotemporal cortex, such as object-selective posterior fusiform sulcus (Kravitz et al., 2010). Body parts primarily occur outside the fovea in the lower visual field, and this may account for the larger size of EBA relative to FBA (Chan, Kravitz, Truong, Arizpe, & Baker, 2010). In addition, a lower-field bias has also been reported in regions of the dorsal visual pathway involved in the visual control of action (Danckert & Goodale, 2003).

In sum, while the specific roles of EBA and FBA in person perception are unclear, the underlying visual field biases in these regions must be taken into account in any theory of their relative functional roles. These underlying visual field biases may reflect the developmental and evolutionary origin of EBA and FBA. More data are needed to test the hierarchical account and clarify the nature of the underlying visual field biases.

* * *

The extrastriate body area (EBA): One structure, multiple functions?

Floris P. de Lange and Harold Bekkering

Radboud University Nijmegen, Donders Institute for Brain, Cognition, and Behavior, Nijmegen, The Netherlands

E-mail: floris.delange@donders.ru.nl

<http://dx.doi.org/10.1080/17588928.2011.604724>

Abstract: Downing and Peelen argue that the extrastriate body area (EBA) creates an unelaborated visual representation of the human body, but is not implicated in any higher-order computational process. We believe that this reflects an outdated view of brain function, in which neural regions are informationally encapsulated modules with fixed computational properties. In contrast, there is mounting evidence that functional properties may not be fixed but may be dependent on the context in which the region is recruited. We will illustrate this by taking a closer look at a visual area of which the properties are potentially even simpler: the primary visual cortex.

The ultimate goal of science is to reduce complexity. In this regard, Downing and Peelen do science a service, by “taking a deliberately simple account of occipitotemporal body representations as far as possible” (p. 203). The claim of Downing and Peelen is that EBA and FBA are not involved in any high-level functions such as perceiving body identity or action goals, but only encode fine details about visually perceived bodies. While we do not contest the importance of these regions for visual encoding of perceived bodies, we take issue with the notion that these regions have no functional relevance beyond this. In particular, we feel that this reflects an outdated view of brain function, in which neural computations are time- and context-independent, whereas mounting evidence paints a more dynamic picture of neuronal computations. We will illustrate this with an example from an earlier visual cortical region, the primary visual cortex (V1).

Since the time of Hubel and Wiesel (1968), V1 has been traditionally thought of as an “edge detector” or spatial filter, given that V1 neurons are exquisitely tuned to both the retinotopic location and spatial orientation of a visual stimulus (e.g., Bell & Sejnowski, 1997). Indeed, the initial response of V1 neurons is very reminiscent of an “edge detector,” with an exquisitely tuned response of each neuron to a particular orientation in a particular part of visual space. This response pattern has been robustly observed both in awake behaving animals and under profound states of anesthesia (Dow, Snyder, Vautin, & Bauer, 1981; Schiller, Finlay, & Volman, 1976).

It may, however, be a mistake to conclude that V1 is only functionally relevant to edge detection. Subsequent studies have shown that V1 response properties (such as orientation and color tuning) can be dramatically different at *later* time points during perceptual inference (Lamme & Roelfsema, 2000). These

changes in response profile, which are likely due to feedback (and possibly horizontal) connections to V1, suggest that V1 computations may be different at different time points. Indeed, computational models of perceptual inference suggest that while early activity in V1 may simply reflect feature detection, at a later stage V1 may actively participate in multiple visual routines such as object reconstruction and completion (Lee, Mumford, Romero, & Lamme, 1998). Indeed, later activity in V1 appears to reflect the perception of illusory contours in Kanisza-like figures, where no physical line is present in the neuron's receptive field (Lee & Nguyen, 2001), and it has even been argued that feedback to V1 is necessary in order to become aware of a visual stimulus (Lamme, 2006; Pascual-Leone & Walsh, 2001). Finally, a recent study provides compelling evidence for a potential role of V1 in working memory, when a visual stimulus had to be held online for a prolonged period of time while the stimulus is not physically present (Harrison & Tong, 2009). Considering all the evidence, the label of V1 as an "edge detector" may at best be an incomplete characterization of this cortical module. While this label may correctly describe the function of this node at an early stage of the cortical computation, when receiving information from the lateral geniculate nucleus in the thalamus, its response properties and thereby putative computational role appear to change at later stages when it receives input from other areas that are higher in the cortical hierarchy.

The same argument may well pertain to the EBA and FBA. There is indeed good evidence of these regions' involvement in the encoding of fine details of bodies (Downing, Jiang, Shuman, & Kanwisher, 2001), just as there is good evidence of the involvement of V1 in encoding orientation and contrast of line stimuli (Hubel & Wiesel, 1968). But there appears equally good evidence of the modulation of activity of these regions by more high-level factors. Indeed, Downing and Peelen describe several cases in which EBA/FBA activity is modulated by higher-level factors. They interpret these activity modulations as "attentional feedback to occipitotemporal cortex" (p. 203). However, as we have seen with the example of V1, activity modulations by feedback may subserve much more complex processing than simply "boosting the representation," and may alter the representation itself. The activity of V1 to an illusory (Lee & Nguyen, 2001) line is "cognitively elaborated," in the sense that it does not passively represent "what the eyes tell," but rather what is in "the mind's eye." It may be equally

incorrect to refer to the representation in EBA as "cognitively unelaborated."

Perhaps the most striking examples of top-down influence on EBA are provided by motor control studies, in which no visual stimulus of a body part were presented, yet where robust EBA activity is sometimes observed (Astafiev, Stanley, Shulman, & Corbetta, 2004; Kuhn, Keizer, Rombouts, & Hommel, 2011; Zimmermann, Meulenbroek, & de Lange, 2011). This situation is reminiscent of the aforementioned study by Harrison and Tong (2009), where, in the absence of any physical stimulus, V1 contributes to holding online a perceptual representation. We believe that EBA may have a similar role in motor control, in terms of holding online a visual representation of the goal state of an action. While this does not contest a role of EBA in representing bodies, it does not render the region irrelevant to motor planning. A crucial test of the necessity of this region in action planning should come from intervention studies, such as lesion studies or transcranial magnetic stimulation (TMS). Indeed, a patient study observed deficits in motor planning following lesions of the ventral occipitotemporal cortex (Dijkerman, McIntosh, Schindler, Nijboer, & Milner, 2009), though the relative lack of specificity precludes a straightforward interpretation. Importantly, TMS studies that aim to show the (ir)relevance of EBA to motor control should bear in mind the potential dynamic nature of the computations in EBA, possibly by targeting this area at different stages of the planning process (cf. Pascual-Leone & Walsh, 2001). We believe that this could be a fruitful area of future research.

* * *

Functional and epiphenomenal modulation of neural activity in body-selective visual areas

Cosimo Urgesi¹ and Alessio Avenanti²

¹Dipartimento di Scienze Umane, Università di Udine, Udine, Italy; and Istituto di Ricovero e Cura a Carattere Scientifico "Eugenio Medea", Polo Friuli Venezia Giulia, Pordenone, Italy

²Dipartimento di Psicologia, Alma Mater Studiorum – Università di Bologna, Bologna, Italy; and Centro

Studi e Ricerche in Neuroscienze Cognitive, Polo Scientifico-Didattico di Cesena, Alma Mater Studiorum – Università di Bologna, Cesena, Italy
E-mail: cosimo.urgesi@uniud.it

<http://dx.doi.org/10.1080/17588928.2011.604725>

Abstract: Although attention may play a major role in explaining EBA/FBA activation during high-order, body-related tasks, it is important to establish the functional significance of top-down modulation in different tasks. While neuroimaging studies documented the functional and anatomical specificity of EBA/FBA activation during body form perception, repetitive transcranial magnetic stimulation (rTMS) and brain-lesion studies provided causative evidence that activity in EBA is essential for processing morphological details of body parts. Local processing of body shapes in EBA might contribute to the representation of high-order body attributes, including person identity and body esthetics, which probably rely on a widespread network of different interconnected areas.

After the first descriptions, 10 years ago, of body-selective activations in the occipitotemporal cortex (Downing, Jiang, Shuman, & Kanwisher, 2001), several studies have now documented modulations of EBA and/or FBA in different tasks involving the visual processing of whole human bodies and non-facial body parts. In their discussion paper, Downing and Peelen review most of this evidence and suggest that the variety of functions involving the body-selective activation of EBA/FBA points to a basic, but still body-specific, perceptual role. Moreover, they propose that the modulation of EBA/FBA neural activity during high-order processing of body stimuli might be attributed to increased attention to the body triggered by task demands. The attentional account is extremely powerful in that it may immediately explain EBA/FBA involvement in high-order functions found in several studies.

We believe, however, that the functional significance of top-down modulation in the different tasks needs to be established. Indeed, attentional top-down modulations of neural activity may be epiphenomenal to task performance, reflecting the increased perceptual saliency of body stimuli in the visual scene or the activity of high-order interconnected areas. Alternatively, it

might have a specific functional significance, reflecting an increased recruitment of areas that process stimulus features critical for task performance.

Disentangling whether increased activation of EBA/FBA during high-order, body-related tasks is functionally essential, rather than epiphenomenal, requires direct testing. It is then critical to understand the following: (1) which body-related, high-order tasks modulate activity in EBA/FBA; (2) to what extent different body-related areas in temporal, parietal, and premotor regions are modulated by high-order tasks; (3) which high-order functions are impaired after damage to EBA/FBA.

Previous neuroimaging studies have provided evidence that modulation of EBA/FBA during at least some high-order cognitive functions is functionally (point 1) and anatomically (point 2) specific. For example, while it is likely that a moving body is more interesting than a still body, EBA activity is not modulated by the movement of the observed body (Downing et al., 2001). Conversely, EBA activity is strongly influenced by distortions in body size (Mohr et al., 2011) and is altered in patients with eating disorders (Suchan et al., 2010; Uher et al., 2005). Furthermore, while perception of incoherent, as compared to coherent, sequences of body postures induces greater activation of EBA, the opposite pattern was found in premotor and parietal areas involved in action representation (Downing, Peelen, Wiggett, & Tew, 2006).

An important contribution to understanding the functional significance of EBA/FBA relies on testing the consequences of their lesion in brain-damaged patients or in neurologically intact individuals by repetitive transcranial magnetic stimulation (rTMS) (point 3) (Avenanti & Urgesi, 2011). Dysfunctional activity of EBA/FBA is associated with deficits in the visual discrimination of body parts, but not of face or object parts (Moro et al., 2008; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Urgesi, Berlucchi, & Aglioti, 2004). Importantly, lesions to EBA/FBA led to poor performance when discriminating the morphology of the body parts of different individuals, while performance in discriminating limb postures with different possible or impossible implied actions was not affected (Candidi, Urgesi, Ionta, & Aglioti, 2008; Moro et al., 2008; Urgesi, Candidi, Ionta, & Aglioti, 2007).

This would suggest that EBA may help to discriminate different body identities, probably by processing the local details of body parts which are stable across the range of postural configurations largely shared by all

The authors are supported by grants from Ministero Italiano della Salute (Progetto Giovani Ricercatori GR-2008-1137139; to C.U.) and the Istituto Italiano di Tecnologia (SEED 2009 Protocol Number 21538 to C. U. and A. A.).

human bodies. Accordingly, rTMS of EBA disrupted the local processing of inverted body postures, but not the configural processing of upright bodies (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). Local versus configural body processing may be involved in different perceptual and high-order tasks, including person discrimination (Urgesi, Candidi et al., 2007) and evaluation of body esthetics (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010). Claiming that EBA/FBA is involved in a high-order body function does not necessarily imply that it explicitly and specifically represents high-order body attributes (such as identity, action, emotion, or esthetics), but rather that EBA/FBA contributes to the representation of such attributes.

It is likely that high-order body attributes are not unitarily represented in a single brain area, but involve a network of regions, each processing specific aspects. For example, body identity may emerge from the integration of different static (e.g., body shape) and dynamic (e.g., gait) perceptual cues with person-specific “semantic” knowledge, including name, occupation, relationships, etc. All these types of information are processed in different interconnected areas, whose pattern of activation might lead to the representation of person-specific identity. This view is in keeping with Downing and Peelen’s proposal, since EBA/FBA is not likely to explicitly represent person identities as whole and unitary attributes (i.e., my romantic partner). This highlights, however, a widespread representation of high-order functions which involves several areas, including EBA/FBA, in processing body shape (the shape of my partner’s body).

Understanding which high-order functions involve EBA or FBA activity will advance our knowledge of body visual representations as well as of the multifaceted organization of complex, body-related functions.

* * *

Faces and bodies in the brain

Giovanni Berlucchi

Neurological Sciences, University of Verona,
Verona, Italy

E-mail: giovanni.berlucchi@univr.it

<http://dx.doi.org/10.1080/17588928.2011.613986>

Abstract: The discovery of face-sensitive and body-sensitive regions in the extrastriate human cortex has raised the problem of the relations of these areas to face and body knowledge and their role in person identification. In this commentary, I point to some as yet unexplored aspects of these cortical regions, including their status as proper anatomo-functional areas, the role of body appearance in the recognition of persons, and the development of body-related and face-related areas in sighted and congenitally blind individuals.

Downing and Peelen (henceforth D&P) present an extensive review of the explosion of studies on body-selective activities of the occipito-temporal cortex which has followed the discovery of the extrastriate body area (EBA) and the fusiform body area (FBA). Both of these areas respond to the visual presentation of bodies and bodily parts except the face. D&P argue that activities in these areas are sufficient to describe the shape and posture of bodies in some detail. More elaborate analyses of bodily structure, actions, and emotional expressions, eventually leading to person identification, are thought by D&P to be carried out in other parts of the brain. This reasonable hypothesis does not exclude the possibility that inputs from EBA and FBA to the putative higher-order areas, as well as feedback from the latter areas to the former, are essential for person identification from bodily appearance and related cognitive abilities. Unfortunately, the psychophysiology of the identification of a person from his/her bodily rather than facial features is not well understood. Bodies are usually covered by clothes and carry paraphernalia which may contribute to or even be essential for person identification, and the face is regarded by most as the paramount if not the only part of human anatomy which allows the recognition of an individual. In her book on visual agnosia, Martha Farah (2004) mentions the old story of the professor walking by two naked students sunbathing, the smarter of whom covers her face instead of her pudenda to avoid being recognized. There is a well-known neurological syndrome of prosopagnosia, the inability to recognize familiar faces, but I am unaware of neurological disorders of person identification specifically based on a faulty appreciation of bodily appearance. In what follows, I will comment on a few questions that have come to my mind while reading the review and will attempt to point to possible experiments that may answer them.

So far, we have little or no cytoarchitectural or hodological information that may confer on EBA and FBA

the status of cortical areas in a strictly anatomofunctional sense. As acknowledged by D&P, the work of Orlov, Makin, and Zohary (2010) suggests that EBA and FBA, as identified by fMRI, may simply represent peaks of activity within a broader cortical territory involved in the processing of environmental information, including the category of bodies and bodily parts, but extending beyond it. Since EBA is known to respond not only to visual inputs but also to proprioceptive inputs from the body (e.g., Astafiev, Stanley, Shulman, & Corbetta, 2004), its characterization as a cortical area would be strengthened by the demonstration of selective inputs to it from the somatosensory thalamus or cortex. In vivo studies with diffusion tensor imaging (DTI) have the potential to provide this information.

Although face recognition is a slowly developing ability (Sugita, 2009), it has long been known that newborn infants are able to distinguish a proper face from a “scrambled” face in which the relative positions of eyes, nose, and mouth are rearranged in a random fashion. By contrast, the ability to distinguish proper bodies from scrambled bodies does not emerge until the middle of the second year, suggesting that knowledge of the basic bodily structure is acquired through postnatal neural maturation or experience or both (Slaughter & Heron, 2004). In affective social exchanges with their mothers, babies most probably pay more attention to emotional visual and acoustic signals from the mother’s face than to signals from her body. Further, the capacity of newborn babies to imitate gestures (Meltzoff & Moore, 1977), if it exists, is limited to the orofacial territory and possibly only to tongue protrusion (Jones, 2009). All this evidence suggests a possibly differential development of face-sensitive and body-sensitive regions in the human cortex, and I wonder if there is any electrophysiological or fMRI evidence to prove it.

Konorski (1967) was the first to postulate the existence of separate “gnostic units” (neurons or cortical

regions) specifically reactive to various categories of visual stimuli, one of which is the seen position of one’s own limbs. He thought that the putative gnostic units for the latter category are utilized very early in life to build up associations between visual inputs from visible body parts and the proprioceptive sensations from those same parts. Such a combination of visual and somatic inputs may be necessary to construct a correct internal image of one’s own body as well as of other bodies. Congenitally blind children draw and model human bodies less accurately than blindfolded sighted children with regard to both presence and placement of body parts, as well as an exaggerated size attributed to hands and arms, which are their main means of space exploration (Critchley, 1953; Kinsbourne & Lempert, 1980). In sighted adults, processing of the body by EBA and FBA extends beyond the visual modality, since both areas are activated by tactile exploration of human faces and other body parts such as hands and feet (Kitada, Johnsrude, Kochiyama, & Lederman, 2009). Further, again in sighted adults, EBA is activated by one’s own movements made out of view (Astafiev et al., 2004), as well as by haptic and visual imagery of body parts. (Costantini, Urgesi, Galati, Romani, & Aglioti, 2011). It is known that in congenitally blind adults different forms of space perception and representation engage posterior brain areas endowed with visual functions in sighted individuals (e.g., Renier et al., 2010; Ricciardi et al., 2009). I wonder whether face- and body-sensitive areas, including EBA and FBA, can be localized with such stimuli and procedures in congenitally blind adults. If so, one would have to assume a commitment, perhaps even an early one, of these areas to represent the body independently of vision.

* * *

Reply to Commentaries

How might occipitotemporal body-selective regions interact with other brain areas to support person perception?

Paul E. Downing¹ and Marius V. Peelen²

¹Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK

²Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy

We argued in our Discussion Paper for the view that the main functional role of occipitotemporal body-selective regions is to make explicit, via patterns of activity, the shape and posture of perceived bodies, rather than directly representing higher-order person attributes. Much of the commentary was on the question of how activity in other brain areas interacts with activity in EBA and FBA. In this reply, we emphasize that our claims do not imply that EBA and FBA are cognitively impenetrable modules that are driven only by bottom-up input from earlier visual regions. Instead, it is likely that these regions interact heavily with other brain regions, and that their activity is shaped—in limited ways—by both feed-forward and feedback connections. In the context of such large-scale networks, EBA and FBA activity will be most effective at conveying detailed information about the shape and posture of bodies in the current percept.

One common theme was on the minds of the majority of commentators: How do EBA and FBA interact with other areas of the brain, and, in particular, how does the activity of higher-order areas influence and shape the representations in these body-selective regions? Various commentators approach this in different ways and with different emphases. For example, Berlucchi states that “inputs from EBA and FBA to the putative higher-order areas, as well as feedbacks from the latter areas to the former, are essential for person identification from bodily appearance and related cognitive abilities”; Ewbank states that “the relationship between EBA and FBA, and the relationship between these regions and higher-level areas, is likely to be reciprocal, with activity in higher-level areas dynamically shaping responsivity in lower-level regions”; and Ramsey et al. “propose that [EBA and FBA] are a part of a reciprocally connected cortical network that functions to minimize prediction error when making identity inferences.”

Several commentators (Berlucchi; Quadflieg & Rossion; Urgesi & Avenanti) explicitly note that an interaction between higher-order areas and EBA/FBA is compatible with our main proposal that these regions encode the shapes and postures of bodies. However,

such interactions were also raised as a challenge to our proposal that representations in EBA/FBA are “cognitively unelaborated” (see commentaries by Ewbank; de Lange & Bekkering; Quadflieg & Rossion; and Ramsey, Cross, & van Schie). In our Discussion Paper, we did not discuss putative interactions between EBA/FBA and other brain regions in detail, mostly because there is not much evidence to go by (other than evidence for attentional modulation). We speculated (p. 193) that activity in EBA and FBA likely follows the subjective percept rather than the retinal image, and that these regions may therefore be influenced by person identity inferences made in other regions (cf. commentaries of Quadflieg & Rossion and Ramsey et al.). Furthermore, we noted (pp. 197, 199) that visual imagery (and presumably working memory) may activate body representations in EBA/FBA (cf. commentary of de Lange & Bekkering). Finally, rather than proposing that EBA and FBA are “cognitively impenetrable modules” (Ewbank), we proposed (p. 202) that there are good functional arguments for why representations in the perceptual nodes of a network should not be fully penetrable by other parts of the network, again stressing the lack of empirical work in this area. As we will outline below, we

support the idea that higher-order regions influence representations in EBA and FBA beyond attentional modulation (e.g., as in the case of visual imagery). We argue that such top-down influences are nonetheless compatible with our view that these regions primarily encode body shape and body posture rather than higher-order person attributes.

It may be useful to think of EBA and FBA as forming an ad hoc network with other remote brain regions when the current goals or focus of interest is relevant to body perception. The “nodes” of this network each contribute information to the whole, in the form of its patterns of activity. The activity of these nodes will bias and influence each other, so that the network will normally tend to settle on a coherent, mutually consistent state that results in some kind of understanding of the scene. In this context, EBA and FBA activity will, as we have argued, be most effective at conveying detailed information about the shape and posture of the bodies of people in the scene.

While in some ways this representation of body shape and posture might be considered a “low-level” representation, we do not argue that EBA and FBA produce a mere copy of the aspects of the retinal image that come from bodies. Instead, we expect that patterns of activity relate to the subjective body percept, which arises from coordinated activity of many areas. Here are two concrete examples (to our knowledge, the relevant studies do not exist). First, by analogy to “Mooney” (1957) faces, we would expect responses to bodies/body parts to increase in FBA and EBA when a highly schematized image produces a body percept, compared to when it does not. Experiencing the percept of a body will shape the way that individual reduced or ambiguous features are interpreted with a corresponding effect on patterns of activity in these regions. Second, prior knowledge about a perceived individual can strongly influence the percept of a person, and likewise the patterns of activity in EBA/FBA. For example, consider a scenario where a person is seen but is partially occluded or otherwise covered, as by loose clothing. Where that person is known to the observer, we would expect a more detailed, focused pattern of response in EBA/FBA reflecting the knowledge of that shape, compared to an unknowing observer.

This second example in particular raises the question of how, and to what extent, body representations in EBA and FBA are “penetrable”; that is, how their activity is modulated or shaped by the influences of other brain regions. The simplest possibility is that overall activity in these regions is grossly up- or down-regulated via such mechanisms as spatial attention (e.g., attending toward or away from the person in a scene). In our Discussion Paper, we argued for such a

mechanism as an alternative account to explain modulations that authors had taken as evidence for more complex processes in these regions. More subtly, similar mechanisms could come into play to select among possible distinct body representations. For example, switching attention from someone’s hand to their foot may not change overall activity levels in EBA but may influence the detailed pattern of activity that is expressed in that region. Finally, activity in other areas may help to “complete” a missing percept, or, similarly, to form a prediction about an upcoming percept. To return to our earlier example: Where an unknown person in an unfamiliar setting is seen, but is partly occluded, local associative processes may be sufficient to complete a general but imprecise representation that would “fill in” the missing stimulus details. Where contextual information or other cues about the identity of the person are available (e.g., through the face), these may further support such completion processes, allowing a more detailed and accurate completion of the missing information.

These proposals allow EBA and FBA to play a rich and complex role in the perception of other people, in combination with other areas, yet preserve the parsimonious idea that the patterns of activity local to these areas are tuned to the relatively simple properties of shape and posture. They show how these patterns can work interactively to extract, for example, the identity of the people around us, without directly and locally coding for identity *per se*. Of course, these questions of connectivity and penetrability are not specific to body representation. In neuroimaging studies, many of the recent efforts to answer these questions have focused, for some good reasons, on faces (e.g., Fairhall & Ishai, 2007). As more becomes known about the neural encoding of the appearance of the body, EBA and FBA will provide a valuable additional test bed for hypotheses about local encoding and long-range influences (Ewbank et al., 2011).

Aside from considering connectivity and penetrability of representations, several of the commentaries explore other more specific issues. We focus briefly on two: the distinction between body parts and wholes, and the development of body representations.

Chan and Baker argue that the evidence for a part-based bias to body representations in EBA, relative to FBA, is not iron-clad. We agree, although we note other TMS evidence that is also consistent with this idea (e.g., Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). More broadly, there is increasing evidence that distinctions between the functional properties of EBA and FBA may be usefully understood in reference to similar focal extrastriate representations of faces and of object form more generally. That is, for each of these

kinds, fMRI studies show focal, selective activations that are relatively posterior-lateral (EBA, face-selective OFA, and object-form selective LO) and distinct foci that are relatively ventro-medial (FBA, face-selective FFA, and object-form selective pFs). Across categories, these representations appear to be distinguished in several ways, including among them a bias for part over whole representations in the posterior-lateral regions, and the reverse bias in ventro-medial representations (Taylor & Downing, 2011).

Further, in an earlier paper, Taylor, Wiggett, and Downing (2007) noted that the hierarchical organization of the body into parts is systematic (“fingers,” “arms,” etc.) and asked whether EBA body representations might respect these boundaries, carving at the joints, as it were. Kemmerer valuably points out that linguistic partitions of the body are not culturally universal, so that, at some level at least, what is a natural “part” of the body for one individual may not be so for another. This provokes an interesting question about the susceptibility of part representations in EBA to semantic/linguistic influences. In the spirit of our proposed framework, we might expect no such influence. However, it is possible that these semantic /linguistic influences shape the way that individuals attend to the bodies of others in daily life. If these biases are regular and consistent, it is conceivable that they would in turn shape, over time, the “space” of neural patterns representing the body in these regions.

Slaughter and Berlucchi both comment on the development of body structure knowledge in infants. Evidence for late development of body structure knowledge comes from studies measuring the time infants look at intact versus scrambled bodies (e.g., a body with arms attached to the hips). Initial studies estimated that it is not before 15 months of age that infants’ looking behavior discriminates between intact and scrambled bodies (Slaughter & Heron, 2004). In a later study (Heron & Slaughter, 2010), this was shown to depend on the realism of the stimuli, with the earliest age of discriminating realistic intact from realistic scrambled bodies being around 9 months of age. By

contrast, sensitivity to body motion and goal-directed action appears to develop earlier in life (Bertenthal, 1993; Király, Jovanovic, Prinz, Aschersleben, & Gergely, 2003). According to Slaughter, this developmental dissociation is consistent with our proposed dissociation between EBA and FBA (involved in the encoding of body shape) and other regions involved in the encoding of body motion and action goals. She further suggests that the developmental dissociation implies that certain aspects of higher-level person perception can occur without the information computed by EBA and FBA. While this is an interesting idea, what needs to be shown to complete the link that Slaughter makes is that developing knowledge of body structure relates systematically to increasing sophistication of the body shape/posture representations in EBA/FBA. Without this, it is still unclear whether the relatively late development of body structure knowledge in infants should be interpreted as providing evidence that high-level person perception, such as perceiving action goals, can bypass EBA and FBA. Finally, it is not unlikely that future studies, using more sensitive methods, may reveal body structure knowledge in infants at increasingly younger ages.

To sum up, the simple model of body encoding that we proposed in our Discussion Paper explains a great deal of the current literature and does so parsimoniously. When considering how EBA and FBA work interactively with other brain areas, as they must, we can see how their shape and posture representations could contribute critically to many high-level functions of person perception, such as the identification of others. Much remains to be learned about how these two areas make distinct contributions to person perception. More generally, it is clear that in the next few years there will be a lot of energy directed at the broad question of how the nodes of the brain’s interconnected networks influence each other. The highly focal, well-characterized nature of extrastriate body representations, and the many cognitive and perceptual functions for which the perception of other people is relevant, make these areas worthy of a focus in these ongoing studies.

References from the Discussion Paper, the Commentaries, and the Reply

- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron*, *21*(2), 373–383.
- Aleong, R., & Paus, T. (2010). Neural correlates of human body perception. *Journal of Cognitive Neuroscience*, *22*(3), 482–495.
- 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.
- Amaral, D. G., Behnia, H., & Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience*, *118*(4), 1099–1120.
- Amedi, A., von Kriegstein, K., Van Atteveldt, N. M., Beauchamp, M. S., & Naumer, M. J. (2005). Functional imaging of human crossmodal identification and object recognition. *Experimental Brain Research*, *166*(3–4), 559–571.
- Anderson, A. K. (2005). Affective influences on the attentional dynamics supporting awareness. *Journal of Experimental Psychology: General*, *134*(2), 258–281.
- Appelbaum, L. G., Wade, A. R., Vildavski, V. Y., Pettet, M. W., & Norcia, A. M. (2006). Cue-invariant networks for figure and background processing in human visual cortex. *Journal of Neuroscience*, *26*, 11695–11708.
- Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, *26*(31), 8074–8081.
- Aslin, R. (2009). How infants view natural scenes gathered from a head-mounted camera. *Optometry and Vision Science*, *86*, 561–565.
- 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.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2005). Is the extrastriate body area involved in motor actions? Reply. *Nature Neuroscience*, *8*(2), 125–126.
- 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*(6), 717–746.
- Avenanti, A., & Urgesi, C. (2011). Understanding 'what' others do: Mirror mechanisms play a crucial role in action perception. *Social Cognitive and Affective Neuroscience*, *6*, 257–259.
- Avikainen, S., Liuhanen, S., Schurmann, M., & Hari, R. (2003). Enhanced extrastriate activation during observation of distorted finger postures. *Journal of Cognitive Neuroscience*, *15*(5), 658–663.
- Bach, P., Peelen, M. V., & Tipper, S. P. (2010). On the role of object information in action observation: An fMRI study. *Cerebral Cortex*, *20*(12), 2798–2809.
- Bar, M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *364*, 1235–1243.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–645.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, *34*(1), 149–159.
- Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., & Saxe, R. (2008). Concepts are more than percepts: The case of action verbs. *Journal of Neuroscience*, *28*(44), 11347–11353.
- Bekkering, H., & Neggers, S. F. (2002). Visual search is modulated by action intentions. *Psychological Science*, *13*(4), 370–374.
- Bell, A. J., & Sejnowski, T. J. (1997). The "independent components" of natural scenes are edge filters. *Vision Research*, *37*, 3327–3338.
- Benuzzi, F., Lui, F., Duzzi, D., Nichelli, P. F., & Porro, C. A. (2008). Does it look painful or disgusting? Ask your parietal and cingulate cortex. *Journal of Neuroscience*, *28*(4), 923–931.
- Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research*, *200*(1), 25–35.
- Bertenthal, B. (1993). Infants' perception of biomechanical motions: Intrinsic image and knowledge-based constraints. In C. E. Granrud (Ed.), *Visual perception and cognition in infancy* (pp. 175–214). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, *58*, 47–73.
- Blanke, O., Ionta, S., Fornari, E., Mohr, C., & Maeder, P. (2010). Mental imagery for full and upper human bodies: Common right hemisphere activations and distinct extrastriate activations. *Brain Topography*, *23*(3), 321–332.
- Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural responses to hands and non-hand body parts in human left extrastriate visual cortex. *Journal of Neurophysiology*, *103*(6), 3389–3397.
- Brandman, T., & Yovel, G. (2010). The body inversion effect is mediated by face-selective, not body-selective, mechanisms. *Journal of Neuroscience*, *30*(31), 10534–10540.
- Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the 'spotlight' of visual attention. *Nature Neuroscience*, *2*(4), 370–374.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, *77*(Pt 3), 305–327.
- Bruner, J. (1973). *Going beyond the information given*. New York, NY: Norton.
- 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.
- Candidi, M., Urgesi, C., Ionta, S., & Aglioti, S. M. (2008). Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. *Social Neuroscience*, *3*(3–4), 388–400.
- Carter, E. J., & Pelphrey, K. A. (2008). Friend or foe? Brain systems involved in the perception of dynamic signals of menacing and friendly social approaches. *Social Neuroscience*, *3*(2), 151–163.

- Chaminade, T., Meltzoff, A. N., & Decety, J. (2005). An fMRI study of imitation: Action representation and body schema. *Neuropsychologia*, *43*(1), 115–127.
- Chan, A. W., Kravitz, D. J., Truong, S., Arizpe, J., & Baker, C. I. (2010). Cortical representations of bodies and faces are strongest in commonly experienced configurations. *Nature Neuroscience*, *13*(4), 417–418.
- Chan, A. W., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *Neuroreport*, *15*(15), 2407–2410.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Cikara, M., Eberhardt, J. L., & Fiske, S. T. (2011). From agents to objects: Sexist attitudes and neural responses to sexualized targets. *Journal of Cognitive Neuroscience*, *23*(3), 540–551.
- Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., et al. (2005). Neural systems underlying observation of humanly impossible movements: An fMRI study. *Cerebral Cortex*, *15*(11), 1761–1767.
- 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.
- Critchley, M. (1953). Tactile thought, with special reference to the blind. *Brain*, *76*, 19–35.
- Cross, E. S., Mackie, E. C., Wolford, G., & Hamilton, A. F. (2010). Contorted and ordinary body postures in the human brain. *Experimental Brain Research*, *204*(3), 397–407.
- Danckert, J. A., & Goodale, M. A. (2003). Ups and downs in the visual control of action. In S. H. Johnson-Frey (Ed.), *Taking action: Cognitive neuroscience perspectives on intentional acts* (pp. 29–64). Cambridge, MA: MIT Press.
- David, N., Cohen, M. X., Newen, A., Bewernick, B. H., Shah, N. J., Fink, G. R., et al. (2007). The extrastriate cortex distinguishes between the consequences of one's own and others' behavior. *NeuroImage*, *36*(3), 1004–1014.
- David, N., Jansen, M., Cohen, M. X., Osswald, K., Molnar-Szakacs, I., Newen, A., et al. (2009). Disturbances of self-other distinction after stimulation of the extrastriate body area in the human brain. *Social Neuroscience*, *4*(1), 40–48.
- David, S. V., Hayden, B. Y., Mazer, J. A., & Gallant, J. L. (2008). Attention to stimulus features shifts spectral tuning of V4 neurons during natural vision. *Neuron*, *59*, 509–521.
- De Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology*, *18*(6), 454–457.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, *4*(8), 2051–2062.
- Devue, C., Collette, F., Balteau, E., Dequeldre, C., Luxen, A., Maquet, P., et al. (2007). Here I am: The cortical correlates of visual self-recognition. *Brain Research*, *1143*, 169–182.
- Dijkerman, H. C., McIntosh, R. D., Schindler, I., Nijboer, T. C. W., & Milner, A. D. (2009). Choosing between alternative wrist postures: Action planning needs perception. *Neuropsychologia*, *47*(7), 1476–1482.
- Dow, B. M., Snyder, A. Z., Vautin, R. G., & Bauer, R. (1981). Magnification factor and receptive field size in foveal striate cortex of the monkey. *Experimental Brain Research*, *44*(7), 213–228.
- Downing, P., Liu, J., & Kanwisher, N. (2001). Testing cognitive models of visual attention with fMRI and MEG. *Neuropsychologia*, *39*(12), 1329–1342.
- Downing, P. E., Chan, A. W., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, *16*(10), 1453–1461.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. G. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470–2473.
- Downing, P. E., Peelen, M. V., Wiggett, A. J., & Tew, B. D. (2006). The role of the extrastriate body area in action perception. *Social Neuroscience*, *1*(1), 52–62.
- Downing, P. E., Wiggett, A. J., & Peelen, M. V. (2007). Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *Journal of Neuroscience*, *27*(1), 226–233.
- Drucker, D. M., & Aguirre, G. K. (2009). Different spatial scales of shape similarity representation in lateral and ventral LOC. *Cerebral Cortex*, *19*(10), 2269–2280.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*(6676), 598–601.
- Ewbank, M. P., Lawson, R. P., Henson, R. N., Rowe, J. B., Passamonti, L., & Calder, A. J. (2011). Changes in “top-down” connectivity underlie repetition suppression in the ventral visual pathway. *Journal of Neuroscience*, *31*(15), 5635–5642.
- Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. *Cerebral Cortex*, *17*(10), 2400–2406.
- Farah, M. J. (2004). *Visual agnosia*. Cambridge, MA: MIT Press.
- Flaisch, T., Schupp, H. T., Renner, B., & Junghofer, M. (2009). Neural systems of visual attention responding to emotional gestures. *NeuroImage*, *45*(4), 1339–1346.
- Friston, K. J. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *360*(1456), 815–836.
- Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(6), 3314–3319.
- 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.
- Georgieff, N., & Jeannerod, M. (1998). Beyond consciousness of external reality: A “who” system for consciousness of action and self-consciousness. *Consciousness and Cognition*, *7*(3), 465–477.
- Ghuman, A. S., McDaniel, J. R., & Martin, A. (2010). Face adaptation without a face. *Current Biology*, *20*(1), 32–36.

- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, 4(3), 179–192.
- Grafton, S. T., & Hamilton, A. F. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science*, 26(4), 590–616.
- Graziano, M. S., & Aflalo, T. N. (2007). Rethinking cortical organization: Moving away from discrete areas arranged in hierarchies. *Neuroscientist*, 13(2), 138–147.
- Grezes, J., Pichon, S., & de Gelder, B. (2007). Perceiving fear in dynamic body expressions. *NeuroImage*, 35(2), 959–967.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Science*, 10(1), 14–23.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24(1), 187–203.
- Grosbras, M. H., & Paus, T. (2006). Brain networks involved in viewing angry hands or faces. *Cerebral Cortex*, 16(8), 1087–1096.
- Gross, C. G. (1992). Representation of visual stimuli in inferior temporal cortex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 335(1273), 3–10.
- 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.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35(6), 1167–1175.
- Gu, X., Liu, X., Guise, K. G., Naidich, T. P., Hof, P. R., & Fan, J. (2010). Functional dissociation of the frontoinsula and anterior cingulate cortices in empathy for pain. *Journal of Neuroscience*, 30(10), 3739–3744.
- Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology*, 13(24), 2201–2205.
- Hamann, S., Herman, R. A., Nolan, C. L., & Wallen, K. (2004). Men and women differ in amygdala response to visual sexual stimuli. *Nature Neuroscience*, 7(4), 411–416.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, 458(7238), 632–635.
- 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.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. A. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–233.
- Haynes, J. D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, 7(7), 523–534.
- Henson, R. N. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70(1), 53–81.
- Heron, M., & Slaughter, V. (2010). Infants' responses to real humans and representations of humans. *International Journal of Behavioral Development*, 34(1), 34–45.
- Hinton, G. E., McClelland, J. L., & Rumelhart, D. E. (1986). Distributed representations. In D. E. Rumelhart & J. L. McClelland (Eds.), *Parallel distributed processing: Explorations in the microstructure of cognition* (pp. 77–109). Cambridge, MA: MIT Press.
- Hirai, M., & Hiraki, K. (2005). An event-related potentials study of biological motion perception in human infants. *Brain Research. Cognitive Brain Research*, 22, 301–304.
- 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.
- Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. *Human Brain Mapping*, 30(3), 951–962.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215–243.
- Ishizu, T., Amemiya, K., Yumoto, M., & Kojima, S. (2010). Magnetoencephalographic study of the neural responses in body perception. *Neuroscience Letters*, 481(1), 36–40.
- 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.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *NeuroImage*, 31(1), 429–439.
- Jastorff, J., & Orban, G. A. (2009). Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing. *Journal of Neuroscience*, 29(22), 7315–7329.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, 14, 201–211.
- Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron*, 39(6), 1053–1058.
- Jones, S. S. (2009). The development of imitation in infancy. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 364, 2325–2335.
- Kable, J. W., & Chatterjee, A. (2006). Specificity of action representations in the lateral occipitotemporal cortex. *Journal of Cognitive Neuroscience*, 18(9), 1498–1517.
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, 8(5), 679–685.
- 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.
- Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, 282(5386), 108–111.

- Kelly, M. H., & Freyd, J. J. (1987). Explorations of representational momentum. *Cognitive Psychology*, *19*(3), 369–401.
- Kemmerer, D., & Tranel, D. (2008). Searching for the elusive neural substrates of body part terms: A neuropsychological study. *Cognitive Neuropsychology*, *25*(4), 601–629.
- Kiefer, M., & Pulvermüller, F. (2011). Conceptual representations in mind and brain: Theoretical developments, current evidence, and future directions. *Cortex*. Advance online publication. doi: 10.1016/j.cortex.2011.04.006.
- Kilner, J., Friston, K., & Frith, C. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, *8*(3), 159–166.
- Kinsbourne, M., & Lempert, H. (1980). Human figure representation by blind children. *Journal of General Psychology*, *102*, 33–37.
- Király, I., Jovanovic, B., Prinz, W., Aschersleben, G., & Gergely, G. (2003). The early origins of goal attribution in infancy. *Consciousness and Cognition*, *12*, 752–769.
- 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.
- Kokal, I., Gazzola, V., & Keysers, C. (2009). Acting together in and beyond the mirror neuron system. *NeuroImage*, *47*(4), 2046–2056.
- Konorski, J. (1967). *Integrative activity of the brain: An interdisciplinary approach*. Chicago, IL: University of Chicago Press.
- Kontariss, I., Wiggett, A. J., & Downing, P. E. (2009). Dissociation of extrastriate body and biological-motion selective areas by manipulation of visual-motor congruency. *Neuropsychologia*, *47*(14), 3118–3124.
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*(1), 48–55.
- Kravitz, D. J., Kriegeskorte, N., & Baker, C. I. (2010). High-level visual object representations are constrained by position. *Cerebral Cortex*, *20*(12), 2916–2925.
- Kret, M. E., Pichon, S., Grezes, J., & de Gelder, B. (2011). Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *NeuroImage*, *54*(2), 1755–1762.
- Kriegeskorte, N., Formisano, E., Sorger, B., & Goebel, R. (2007). Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(51), 20600–20605.
- Kuhn, S., Keizer, A., Rombouts, S. A., & Hommel, B. (2011). The functional and neural mechanism of action preparation: Roles of EBA and FFA in voluntary action control. *Journal of Cognitive Neuroscience*, *23*(1), 214–220.
- 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.
- Lamme, V. A. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *107*, 494–501.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *I. Trends in Neuroscience*, *237*, 571–579.
- Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *Journal of Neuroscience*, *26*(11), 2894–2906.
- Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. (1998). The role of the primary visual cortex in higher level vision. *Vision Research*, *387*, 2429–2454.
- Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *987*, 1907–1911.
- Leube, D. T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. (2003). The neural correlates of perceiving one's own movements. *NeuroImage*, *20*(4), 2084–2090.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, *4*(5), 533–539.
- 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.
- Lorteije, J. A., Barraclough, N. E., Jellema, T., Raemaekers, M., Duijnhouwer, J., Xiao, D., et al. (2011). Implied motion activation in cortical area MT can be explained by visual low-level features. *Journal of Cognitive Neuroscience*, *23*(6), 533–548.
- Macrae, C. N., & Quadflieg, S. (2010). Perceiving people. In S. Fiske, D. T. Gilbert, & G. Lindzey (Eds.), *The handbook of social psychology* (5th ed., pp. 428–463). New York, NY: McGraw-Hill.
- Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., & Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron*, *63*(3), 397–405.
- Majid, A. (2010). Words for parts of the body. In B. Malt & P. Wolff (Eds.), *Words and the mind* (pp. 58–71). Oxford, UK: Oxford University Press.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(18), 8135–8139.
- Marsh, A. A., Kozak, M. N., Wegner, D. M., Reid, M. E., Yu, H. H., & Blair, R. J. (2010). The neural substrates of action identification. *Social Cognitive and Affective Neuroscience*, *5*(4), 392–403.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, *58*, 25–45.
- Maunsell, J. H., & Van Essen, D. C. (1987). Topographic organization of the middle temporal visual area in the macaque monkey: Representational biases and the relationship to callosal connections and myeloarchitectonic boundaries. *Journal of Comparative Neurology*, *266*(4), 535–555.
- Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, *198*, 75–78.
- Michels, L., Kleiser, R., de Lussanet, M. H. E., Seitz, R. J., & Lappe, M. (2009). Brain activity for peripheral biological motion in the posterior superior temporal gyrus and the

- fusiform gyrus: Dependence on visual hemifield and view orientation. *NeuroImage*, 45(1), 151–159.
- Michels, L., Lappe, M., & Vaina, L. M. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. *Neuroreport*, 16(10), 1037–1041.
- Minnebusch, D. A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. *Neuroscience and Biobehavioral Reviews*, 33(7), 1133–1144.
- Minnebusch, D. A., Suchan, B., & Daum, I. (2009). Losing your head: Behavioral and electrophysiological effects of body inversion. *Journal of Cognitive Neuroscience*, 21(5), 865–874.
- Mohr, C., Porter, G., & Benton, C. P. (2007). Psychophysics reveals a right hemispheric contribution to body image distortions in women but not men. *Neuropsychologia*, 45(13), 2942–2950.
- Mohr, H. M., Röder, C., Zimmermann, J., Hummel, D., Negele, A., & Grabhorn, R. (2011). Body image distortions in bulimia nervosa: Investigating body size overestimation and body size satisfaction by fMRI. *NeuroImage*, 56, 1822–1831.
- Molenberghs, P., Brander, C., Mattingley, J. B., & Cunnington, R. (2010). The role of the superior temporal sulcus and the mirror neuron system in imitation. *Human Brain Mapping*, 31(9), 1316–1326.
- Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology*, 11(4), 219–226.
- 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), 235–246.
- Morrison, I., & Downing, P. E. (2007). Organization of felt and seen pain responses in anterior cingulate cortex. *NeuroImage*, 37(2), 642–651.
- 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.
- Morrison, I., Peelen, M. V., & Downing, P. E. (2007). The sight of others' pain modulates motor processing in human cingulate cortex. *Cerebral Cortex*, 17(9), 2214–2222.
- Morris, J. P., Pelphrey, K. A., & McCarthy, G. (2006). Occipitotemporal activation evoked by the perception of human bodies is modulated by the presence or absence of the face. *Neuropsychologia*, 44(10), 1919–1927.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121(Pt 1), 47–57.
- Mouras, H., Stoleru, S., Bittoun, J., Glutron, D., Pelegrinialssac, M., Paradis, A. L., et al. (2003). Brain processing of visual sexual stimuli in healthy men: A functional magnetic resonance imaging study. *NeuroImage*, 20(2), 855–869.
- Mumford, D. (1992). On the computational architecture of the neocortex. II. The role of cortico-cortical loops. *Biological Cybernetics*, 66, 241–251.
- Mur, M., Bandettini, P. A., & Kriegeskorte, N. (2009). Revealing representational content with pattern information fMRI—an introductory guide. *Social Cognitive and Affective Neuroscience*, 4(1), 101–109.
- Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. *NeuroImage*, 42(4), 1669–1677.
- Newman-Norlund, R. D., Noordzij, M. L., Meulenbroek, R. G. J., & Bekkering, H. (2007). Exploring the brain basis of joint action: Co-ordination of actions, goals and intentions. *Social Neuroscience*, 2(1), 48–65.
- Nummenmaa, L., Hirvonen, J., Parkkola, R., & Hietanen, J. K. (2008). Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. *NeuroImage*, 43(3), 571–580.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, 401(6753), 584–587.
- O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A., & Savoy, R. L. (1997). Voluntary attention modulates fMRI activity in human MT-MST. *Neuron*, 18(4), 591–598.
- Oosterhof, N. N., Wiggett, A. J., Diedrichsen, J., Tipper, S. P., & Downing, P. E. (2010). Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *Journal of Neurophysiology*, 104(2), 1077–1089.
- Op de Beeck, H. P., Brants, M., Baeck, A., & Wagemans, J. (2010). Distributed subordinate specificity for bodies, faces, and buildings in human ventral visual cortex. *NeuroImage*, 49(4), 3414–3425.
- 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.
- Orlov, T., Makin, T. R., & Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron*, 68(3), 586–600.
- Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, 2927, 510–512.
- 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. (2005a). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608.
- Peelen, M. V., & Downing, P. E. (2005b). Is the extrastriate body area involved in motor actions? *Nature Neuroscience*, 8(2), 125; author reply 125–125; author reply 126.
- Peelen, M. V., & Downing, P. E. (2007a). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8), 636–648.
- Peelen, M. V., & Downing, P. E. (2007b). Using multi-voxel pattern analysis of fMRI data to interpret overlapping functional activations. *Trends in Cognitive Sciences*, 11(1), 4–5.

- Peelen, M. V., Fei-Fei, L., & Kastner, S. (2009). Neural mechanisms of rapid natural scene categorization in human visual cortex. *Nature*, *460*(7251), 94–97.
- Peelen, M. V., Glaser, B., Vuilleumier, P., & Eliez, S. (2009). Differential development of selectivity for faces and bodies in the fusiform gyrus. *Developmental Science*, *12*(6), F16–F25.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, *49*(6), 815–822.
- Peigneux, P., Van der Linden, M., Garraux, G., Laureys, S., Degueldre, C., Aerts, J., et al. (2004). Imaging a cognitive model of apraxia: The neural substrate of gesture-specific cognitive processes. *Human Brain Mapping*, *21*(3), 119–142.
- Peuskens, H., Vanrie, J., Verfaillie, K., & Orban, G. A. (2005). Specificity of regions processing biological motion. *European Journal of Neuroscience*, *21*(10), 2864–2875.
- Piefke, M., Kramer, K., Korte, M., Schulte-Ruther, M., Korte, J. M., Wohischlager, A. M., et al. (2009). Neurofunctional modulation of brain regions by distinct forms of motor cognition and movement features. *Human Brain Mapping*, *30*(2), 432–451.
- Pierno, A. C., Tubaldi, F., Turella, L., Grossi, P., Barachino, L., Gallo, P., et al. (2009). Neurofunctional modulation of brain regions by the observation of pointing and grasping actions. *Cerebral Cortex*, *19*(2), 367–374.
- Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., et al. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(15), 5658–5663.
- Pinsk, M. A., Arcaro, G., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., & Kastner, S. (2009). Neural representations of faces and body parts in macaque and human cortex: A comparative fMRI study. *Journal of Neurophysiology*, *101*, 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 of the United States of America*, *102*(19), 6996–7001.
- 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*, 319–324.
- Ponseti, J., Bosinski, H. A., Wolff, S., Peller, M., Jansen, O., Mehdorn, H. M., et al. (2006). A functional endophenotype for sexual orientation in humans. *NeuroImage*, *33*(3), 825–833.
- Pourtois, G., Peelen, M. V., Spinelli, L., Seeck, M., & Vuilleumier, P. (2007). Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia*, *45*(11), 2621–2625.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letter strings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *16*(16), 5205–5215.
- Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *358*(1431), 435–445.
- Quadflieg, S., Flannigan, N., Waiter, G. D., Rossion, B., Wig, S. G., Turk, D. J., & Macrae, C. N. (2011). Stereotype-based modulation of person perception. *NeuroImage*, *57*, 549–557.
- Ramsey, R., & Hamilton, A. F. (2010). Understanding actors and object-goals in the human brain. *NeuroImage*, *50*(3), 142–1147.
- Reid, V. M., Hoehl, S., & Striano, T. (2006). The perception of biological motion by infants: An event-related potential study. *Neuroscience Letters*, *395*, 211–214.
- Renier, L. A., Anurova, I., De Volder, A. G., Carlson, S., Van Meter, J., & Rauschecker, J. P. (2010). Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. *Neuron*, *68*, 138–148.
- Ricciardi, E., Bonino, D., Sani, L., Vecchi, T., Guazzelli, M., Haxby, J. V., et al. (2009). Do we really need vision? How blind people “see” the actions of others. *Journal of Neuroscience*, *29*(31), 9719–9724.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, *126*(Pt 11), 2381–2395.
- Rueschemeyer, S. A., Pfeiffer, C., & Bekkering, H. (2010). Body schematics: On the role of the body schema in embodied lexical-semantic representations. *Neuropsychologia*, *48*(3), 774–781.
- Sachdev, P., Mondraty, N., Wen, W., & Gulliford, K. (2008). Brains of anorexia nervosa patients process self-images differently from non-self-images: An fMRI study. *Neuropsychologia*, *46*(8), 2161–2168.
- 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.
- Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, *42*(11), 1435–1446.
- Schendan, H. E., & Kutas, M. (2003). Time course of processes and representations supporting visual object identification and memory. *Journal of Cognitive Neuroscience*, *15*(1), 111–135.
- Schiller, P. H., Finlay, B. L., & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex. I. Spatiotemporal organization of receptive fields. *Journal of Neurophysiology*, *39*, 1288–1319.
- 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.
- Schwarzlose, R. F., Swisher, J. D., Dang, S. B., & Kanwisher, N. (2008). The distribution of category and location information across object-selective regions in human visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(11), 4447–4452.

- Schwobel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, *17*(4), 543–553.
- Singer, J. M., & Sheinberg, D. L. (2010). Temporal cortex neurons encode articulated actions as slow sequences of integrated poses. *Journal of Neuroscience*, *30*(8), 3133–3145.
- 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.
- Slaughter, V., & Heron, M. (2004). Origins and early development of human body knowledge. *Monographs of the Society for Research in Child Development*, *69*(2), vii, 1–102.
- Southgate, V., Johnson, M. H., & Csibra, G. (2008). Infants attribute goals even to biomechanically impossible actions. *Cognition*, *107*, 1059–1069.
- 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.
- Spiridon, M., & Kanwisher, N. (2002). How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*, *35*(6), 1157–1165.
- Spunt, R. P., Falk, E. B., & Lieberman, M. D. (2010). Dissociable neural systems support retrieval of how and why action knowledge. *Psychological Science*, *21*(11), 1593–1598.
- Spunt, R. P., Satpute, A. B., & Lieberman, M. D. (2011). Identifying the what, why, and how of an observed action: An fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience*, *23*(1), 63–74.
- Suchan, B., Busch, M., Schulte, D., Gronermeier, D., Herpertz, S., & Vocks, S. (2010). Reduction of gray matter density in the extrastriate body area in women with anorexia nervosa. *Behavioural Brain Research*, *206*(1), 63–67.
- Sugita, Y. (2009). Innate face processing. *Current Opinion in Neurobiology*, *19*, 39–44.
- Sugiura, M., Sassa, Y., Jeong, H., Miura, N., Akitsuki, Y., Horie, K., et al. (2006). Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. *NeuroImage*, *32*(4), 1905–1917.
- Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, *11*(9), 1004–1006.
- Takahashi, H., Shibuya, T., Kato, M., Sassa, T., Koeda, M., Yahata, N., et al. (2008). Enhanced activation in the extrastriate body area by goal-directed actions. *Psychiatry and Clinical Neurosciences*, *62*(2), 214–219.
- Taylor, J. C., & Downing, P. E. (2011). Division of labor between lateral and ventral extrastriate representations of faces, bodies, and objects. *Journal of Cognitive Neuroscience*. Advance online publication. doi: 10.1162/jocn_a_00091.
- Taylor, J. C., Roberts, M. V., Downing, P. E., & Thierry, G. (2010). Functional characterisation of the extrastriate body area based on the N1 ERP component. *Brain and Cognition*, *73*(3), 153–159.
- 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.
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2010). fMRI-adaptation studies of viewpoint tuning in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, *103*(3), 1467–1477.
- 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.
- 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.
- Uher, R., Murphy, T., Friederich, H. C., Dalgleish, T., Brammer, M. J., Giampietro, V., et al. (2005). Functional neuroanatomy of body shape perception in healthy and eating-disordered women. *Biological Psychiatry*, *58*(12), 990–997.
- 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 of the United States of America*, *105*(6), 2209–2213.
- 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.
- Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *Journal of Neuroscience*, *27*, 8023–8030.
- Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, *10*, 30–31.
- Valyear, K. F., & Culham, J. C. (2010). Observing learned object-specific functional grasps preferentially activates the ventral stream. *Journal of Cognitive Neuroscience*, *22*(5), 970–984.
- Van Dam, W. O., Rueschemeyer, S. A., & Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: An fMRI study. *NeuroImage*, *53*(4), 1318–1325.
- Van de Riet, W. A. C., Grezes, 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.
- Van Overwalle, F., & Baetens, K. (2009). Understanding others’ actions and goals by mirror and mentalizing systems: A meta-analysis. *Neuroimage*, *48*(3), 564–584.
- Vocks, S., Busch, M., Gronermeier, 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.
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*(12), 585–594.

- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*(11), 1271–1278.
- 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.
- Weiner, K. S., & Grill-Spector, K. (2010). Sparsely-distributed organization of face and limb activations in human ventral temporal cortex. *NeuroImage*, *52*(4), 1559–1573.
- Weiner, K. 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.
- Whitney, D., Ellison, A., Rice, N. J., Arnold, D., Goodale, M., Walsh, V., et al. (2007). Visually guided reaching depends on motion area MT+. *Cerebral Cortex*, *17*(11), 2644–2649.
- Wiggett, A. J., & Downing, P. E. (2008). The face network: Overextended? (Comment on: “Let’s face it: It’s a cortical network” by Alomit Ishai). *NeuroImage*, *40*(2), 420–422.
- Wiggett, A. J., & Downing, P. E. (2011). Representation of action in occipito-temporal cortex. *Journal of Cognitive Neuroscience*, *23*(7), 1765–1780.
- Willems, R. M., Peelen, M. V., & Hagoort, P. (2010). Cerebral lateralization of face-selective and body-selective visual areas depends on handedness. *Cerebral Cortex*, *20*(7), 1719–1725.
- Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology*, *79*(3), 1574–1578.
- Yomogida, Y., Sugiura, M., Sassa, Y., Wakusawa, K., Sekiguchi, A., Fukushima, A., et al. (2010). The neural basis of agency: An fMRI study. *NeuroImage*, *50*(1), 198–207.
- Yovel, G., Pelc, T., & Lubetzky, I. (2010). It’s all in your head: Why is the body inversion effect abolished for headless bodies? *Journal of Experimental Psychology: Human Perception and Performance*, *36*(3), 759–767.
- Zimmermann, M., Meulenbroek, R. G., & de Lange, F. P. (2011). Motor planning is facilitated by adopting an action’s goal posture: An fMRI study. *Cerebral Cortex*. Advance online publication. doi: 10.1093/cercor/bhr098.