Review

Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions

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ABSTRACT

Recent studies of monkeys and humans have identified several brain regions that respond to bodies. Researchers have so far mainly addressed the same questions about bodies and bodily expressions that are already familiar from three decades of face and facial expression studies. Our present goal is to review behavioral, electrophysiological and neurofunctional studies on whole body and bodily expression perception against the background of what is known about face perception. We review all currently available evidence in more detail than done so far, but we also argue for a more theoretically motivated comparison of faces and bodies that reflects some broader concerns than only modularity or category specificity of faces or bodies.

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1. Introduction

Perception of bodies and bodily expressions is a relatively novel topic in affective neuroscience, a field dominated so far by investigations of facial expressions. Faces and bodies are equally salient and familiar in daily life and often convey some of the same information, leading one to expect that many of the same issues arise about both. Yet research on faces still tends to be dominated by the issue of category specificity. Historically, patients with pure face deficits have proven hard to find and as a consequence the debate on the existence of a pure deficit is still going on. But since the early days of functional brain imaging considerable efforts have been devoted to argue for category specificity as opposed to distributed object representation. Should body researchers follow this well trodden path and focus on uncovering THE body specific brain area(s)? Given the massive evidence positive as well as negative, about categorical representation of faces and the little information we have so far about bodies, it is likely that the case for or against body specificity will remain stronger for faces and this for a long time to come. This is indeed the conclusion reached in a recent paper (Minnebusch and Daum, 2009). Is this the right conclusion?

Our goal here is not only to consider all the available evidence in more detail than done so far but also to argue for a theoretically motivated comparison of faces and bodies that is sensitive to broader issues than only category specificity. Faces, bodies but also many other objects are multidimensional information bearers. Indeed, without a theoretical motivation and a focus on one or a few specific dimensions, it is hard to decide upon the appropriate control category and the results of such somewhat arbitrary comparisons will fail to convince researchers using a different one. For example, emotion expression and action representation are two very important aspects in body representation. The first has an equivalent for faces, but the second does not. But even the equivalence concerning the emotional dimension of face and body stimuli may be less straightforward than it seems. We typically relate a facial expression to mental states and feelings, but we tend to associate a bodily expression with the action a person is involved in. So even if from the vantage point of emotion expression they superficially convey the same affective signals, facial and bodily expressions may trigger very different processes in the observer. The facial expression may predominantly produce empathy in the observer while a bodily expression may be a call for action (de Gelder, 2009). And the stimulus equivalent of a body engaged in a neutral action is also difficult to find in the domain of facial information. For example, neutral facial movements often used as control condition are speech, chewing or making a grimace but each triggers other processes than does the observation of a body crossing the street, gardening or playing tennis, all of which count as neutral events but none of which has a clear equivalent in the face domain.

2. Similarities in perceptual routines: configuration and feature-based perception of faces, bodies and other visual objects

The major concepts used to argue for the specificity of perceptual processes involved in face perception are those of configuration-based vs. feature-based processes. Note that configural and holistic are often used interchangeably now, but for a while the notion of holistic processes referred to the strong claim that in some cases of complex stimuli the composing parts or (misleadingly called) the features are not encoded separately (Farah, 1990) and therefore not available for perceptual processes. The more general notion of configural processes does not make the claim that facial features or parts are not represented. So, at present there is no reason to refer to holistic processes as different from configural ones (see also below) and it is not clear whether this term will be of any future use in body research. In any case, it is also informative to put the questions about configural processing in the broader context of major theories of object perception and relate them to a classical effect in the visual perception literature, the object superiority effects, generally defined as the influence of whole object recognition on recognition of the parts. Configural processing of faces then appears as a kind of object superiority effect. This puts the debate on configural processing in a broader context because the argument cannot be that faces are special because they are processed configurally. It is worth keeping in mind that the very first reports noting this effect (Yin, 1969) already used a large number of visual objects besides faces and reported inversion effects for some of them (e.g. landscapes).

To come back to the question raised earlier, similarities between configural processing of faces and bodies were reported as soon as this issue was addressed. There is clear evidence that both faces and bodies are processed configurally, rather than as an assemblage of features. This is typically assessed by measuring the perceptual processes that are triggered by tasks in which faces are presented upside-down (the inversion effect): faces and bodies presented upside-down are relatively more difficult to recognize than inverted objects, like for example houses (Reed et al., 2003). By and large evidence from brain imaging studies has since confirmed these first findings of a body inversion effect while also providing information about its time course. Here, however, the evidence points to interesting differences with the face inversion effect, as far as time course but also as far as neural generators are concerned (Meeren et al., 2008).
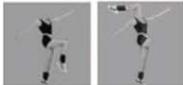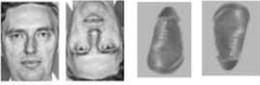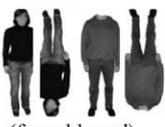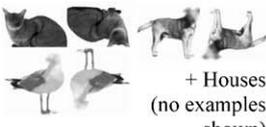
3. The neurophysiology of body perception. Implications for neural representation and time course of processing

Neurophysiological studies of body processing started with single cell recording studies in the monkey. In the late 1960s Gross et al. (1969, 1972) showed neurons in the inferior temporal cortex (IT) that selectively fired to silhouettes of monkey hands, a result which was later confirmed for drawings of human hands and faces (Desimone et al., 1984). Subsequently, neurons responding to static images of whole bodies, body postures that imply some form of body motion, body orientations, and body movements were discovered in superior temporal sulcus (STS) (Perrett et al., 1985; Wachsmuth et al., 1994; Oram and Perrett, 1996; Jellema and Perrett, 2003a, 2003b; Barraclough et al., 2006).

Strong evidence for body shape specificity was found recently by Kiani et al. (2007) who recorded from a large population of single cells in monkey. The response pattern of the cell population as a whole was far more category-selective than that of single cells, implying that not only cell responses to the preferred category but also responses to the suboptimal categories carry important information. The population responses formed category clusters that resembled our intuitive object categories, with a first main division between animals and inanimate objects. The animal-characteristic responses could be divided into face- and body-related responses, and these could be further subdivided on the basis of certain animal classes, with the body population code forming three distinct clusters, i.e. for human bodies, four-limbed animals and birds, and lower animals.

Intracranial recordings from the ventral and lateral temporal cortex in epileptic patients showed a first hint of body-related processing in the human brain with distinct electrode sites being responsive only to photographs of hands and not faces or other objects (McCarthy et al., 1999). Since there is strong evidence for distinct representations of faces, bodies and hands with whole bodies and hands forming completely non-overlapping clusters

Table 1
Overview of the N170 ERP component in body perception studies: stimuli, task, findings.

Study	Body Stimuli (presentation duration)	Non-body stimuli	Task	N170 findings
Scalp EEG				
Stekelenburg & de Gelder, 2004	500ms (faces blurred)		Forced-choice upright vs inverted judgement	AMP: Faces>Bodies; Bodies=Shoes. LAT: Bodies (157ms) < Faces (167ms) TOP: Bodies and Faces very similar, different for Shoes Inversion Effect: Increase in LAT (12 ms) and AMP for both Faces and Bodies
Gliga & Dehaene-Lambertz, 2005	1500ms		Passive viewing	AMP: Bodies = Faces LAT: Bodies (228ms) > Faces (204 ms) TOP: different for faces and bodies Distorted bodies: Decrease in AMP, no LAT effect
Meeren et al., 2005	200 ms emotionally congruent and incongruent face-body compound stimuli		Forced-choice emotion classification of the face (on the body for headless bodies)	AMP: Bodies = Faces LAT: Face-Body compounds (177ms) < Faceless Bodies (187ms) < Faces (199ms) Effects of Bodily Emotion: LAT Angry Bodies (175 ms) < Fearful Bodies (180 ms) in Face-Body Compound stimuli. No effect for Faceless Bodies or Faces.
Thierry et al., 2006	200 ms		1-back repetition detection task	AMP: Faces > Bodies > Objects & Scenes LAT: Bodies (Photos 190ms / Silhouettes 185ms / Stick figures 193ms) > Faces (170ms) TOP: Different for Faces vs. Bodies (photos/silhouettes/stick figures) S_LOC: right posterior extrastriate cortex; larger and more dorsal for Bodies than for Faces.
Righart & de Gelder, 2007	500 ms (faces blurred)		Delayed forced-choice upright vs inverted judgement	AMP: Faces > Bodies LAT: Upright Bodies (155ms) < Upright Faces (165ms) < Upright Shoes (179 ms) Inversion Effect: Increase LAT and AMP for both Faces (13ms) and Bodies (9ms). *Opposite inversion effect* in prosopagnosics for Faces (LAT & AMP in 2/4 patients) and for Bodies (LAT in 2/4, AMP 3/4 patients)
Van Heijnsbergen et al., 2007	700 ms Neutral and Fearful Body postures (faces blurred)		Catch trial detection (white star superimposed on body)	N170/VPP AMP: Bodies >> Scrambles (absent) LAT: Bodies: 175ms (N170) / 177ms (VPP) Fear effect: Decrease in VPP LAT (4ms)
Minnebusch et al., 2009	250 ms Bodies with and without heads (faces blurred)	+ Houses (no examples shown)	Same/different judgement on two consecutive stimuli	AMP: Human & Animal Bodies >> Houses. LAT: No category effect. Inversion Effect: Increase LAT (6 ms) & AMP for Bodies with Heads; *Opposite inversion effect* AMP for Headless Bodies and Cats
Intracranial LFP				
Pourtois et al., 2007	500 ms		Four-alternative forced choice object categorization	Highly spatially-specific body-selective responses on one electrode location within subdural grid. AMP: Headless Bodies >> Faces, Animals, Tools. LAT: surface negative component peaking at 260 ms. LOC: Talairach coordinates responsive electrode (compare with Table 2): x = +39, y =−77, z =−2

All findings are from healthy adults unless stated otherwise. Results on other ERP components (except VPP) and results in infants (Gliga and Dehaene-Lambertz, 2005) are not included here. EEG = electroencephalography; LFP = local field potentials; AMP = amplitude; LAT = latency; TOP = topography; S_LOC = source localization; LOC = location. RH = right hemisphere; LH = left hemisphere.

(Kiani et al., 2007), we will further focus on whole body-selective processing and will not discuss studies on hand perception. Using a subdural grid on the lateral occipital cortex, Pourtois et al. (2007) observed highly spatially specific body-selective responses in the human brain. One electrode site positioned at the junction of the middle temporal and middle occipital gyrus (see Tables 1 and 2 to compare coordinates) showed strong local field potentials peaking at 260 ms elicited by photographs of whole human bodies (without heads) and not by faces, animals or tools.

Further information on the time course of body-selective processing in the human brain has been obtained from non-invasive electrophysiological recordings. The deflections in the Event-Related Potentials (ERPs) of face and body perception show several similarities (Stekelenburg and de Gelder, 2004; Gliga and Dehaene-Lambertz, 2005; Meeren et al., 2005; Thierry et al., 2006; Righart and de Gelder, 2007). ERPs for faces as well as for bodies show a P1 and a prominent N1 component with similar scalp topography (Stekelenburg and de Gelder, 2004). The N1, better known as the "N170" in the case of face processing, a negative deflection at occipitotemporal electrodes peaking between 140 and 220 ms post stimulus onset, is thought to reflect a late stage in the structural encoding of the visual stimulus (Bentin et al., 1996; Eimer, 2000). The mean peak latency of the N1 component for body processing has been found to range between 154 and 228 ms after stimulus onset (Stekelenburg and de Gelder, 2004; Gliga and Dehaene-Lambertz, 2005; Meeren et al., 2005; Thierry et al., 2006; Righart and de Gelder, 2007; van Heijnsbergen et al., 2007; Minnebusch and Daum, 2009), similar as found for faces (see Astafiev et al., 2004; Chan et al., 2004; Downing et al., 2006a,b, 2007; Grosbras and Paus, 2006; Grossman and Blake, 2002; Hadjikhani et al., 2009; Lamm and Decety, 2008; Morris et al., 2006; Peelen and Downing, 2005a; Peelen and Downing, 2005c; Peelen et al., 2006, 2009; Sakreida et al., 2005; Saxe et al., 2006; Van den Stock et al., in preparation; Table 1).

When faces and bodies are directly compared, the peak latency of the N1 for whole human bodies that include heads (with faces masked) was found to be faster than that for faces (Stekelenburg and de Gelder, 2004; Meeren et al., 2005; Righart and de Gelder, 2007). When headless bodies are presented, however, the N1 response slows down to become slower than that for faces (Gliga and Dehaene-Lambertz, 2005; Thierry et al., 2006). When analyzed at a higher spatial resolution, the body and face N1 showed a slightly different spatial pattern, both in their potential distribution on the scalp (Gliga and Dehaene-Lambertz, 2005) and their corresponding source localizations in the brain (Thierry et al., 2006). For both stimulus categories, the sources were located in the right posterior extrastriate cortex, but with a slightly more dorsal distribution for bodies as compared to faces. Different underlying neural generators for face and body perception in the N1 time window were recently confirmed by us using magnetoencephalography (MEG) with anatomically constrained distributed source modeling (Meeren et al., submitted for publication). The ventral inferior temporal cortex, including fusiform gyrus (FG) showed strong differential activation to face stimuli compared to bodies and different classes of control stimuli (i.e. scrambles and houses) between 120 and 180 ms after picture onset. Body stimuli, on the other hand, elicited selective responses in the right lateral occipitotemporal cortex, a location corresponding to the extrastriate body area (EBA) (Downing et al., 2001). No evidence could be found for early activation of the ventral temporal cortex during body perception. These neuromagnetic findings strongly argue against the proposed functional analogies between the face-sensitive and body-sensitive areas in the FG (Taylor et al., 2007; Minnebusch and Daum, 2009).

The well-known electrophysiological inversion effect for faces, i.e. an increase in amplitude and latency of the N170 has also been found for bodies (Stekelenburg and de Gelder, 2004; Righart and de Gelder, 2007; Taylor et al., 2007; Minnebusch and Daum, 2009). The earlier inversion effect as observed for faces on the P1 component (~120 ms), could however not be found for bodies (Righart and de Gelder, 2007). Note in this context that the inversion effect needs to be assessed as the relative difference in latency and amplitude between a given stimulus and its upside-down presented counterpart. Because of the sensitivity of ERP to physical stimulus differences direct comparisons between faces and bodies are misleading. Adopting that criterion we see that the inversion effect is of the same magnitude for faces and bodies (Stekelenburg and de Gelder, 2004).

This matter may be pursued by taking advantage of the sensitive time measurements that MEG provides. We recently investigated the earliest onset of the electrophysiological inversion effect for face and body stimulus categories (Meeren et al., 2008). Anatomically constrained distributed source analyses revealed that both faces and bodies already show inversion effects between 70 and 100 ms post stimulus with larger responses for the inverted images. Interestingly the cortical distribution of this early inversion effect was highly category specific. For faces it was found in well-known face-selective areas (e.g. the right inferior occipital gyrus (IOG) and FG), whereas for bodies it was found in the posterio-dorsal medial parietal areas (the precuneus/posterior cingulate). Hence, whereas face inversion modulates early activity in face-selective areas in the ventral stream, body inversion evokes differential activity in dorsal stream areas, suggesting different early cortical pathways for configural face and body perception, and again different time courses of activation in the common neural substrate in the FG.

Taking together all currently available information on the time course of body and face processes brings us to the conclusion that reports of time courses and a fortiori comparative ones of different visual objects cannot be confined to the presence/absence of a pre-defined marker (e.g. the face specific N170). We need to look at different time windows in different brain areas, some of which also activate during more than a single window.
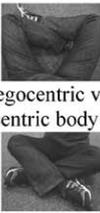
4. Similarities and differences in neurofunctional basis of faces and bodies

This last decade brain imaging has been the method of choice for researchers interested in category specificity. There is evidence that apart from face-selective areas there exist body-selective areas in the brain. In monkeys, functional Magnetic Resonance Imaging (fMRI) revealed specialized patches for faces and bodies within the object-selective cortex (Tsao et al., 2003; Pinsk et al., 2005). In addition, faces and bodies, like the other categories tested, elicited unique distributed response patterns outside these specialized patches (Tsao et al., 2003). Whether these fMRI-defined body areas consist entirely of body-selective cells as was the case for faces (Tsao et al., 2006) remains to be investigated. An important comparative study that builds on the single cell recording study of Kiani et al. (2007) provided evidence for the similarities in object representation in the monkey and the human brain (Kriegeskorte et al., 2008). Computations of dissimilarity for distributed blood oxygenation level dependent (BOLD) response patterns in the human brain revealed that these response patterns form category clusters corresponding to animate and inanimate objects. Within the former, subclusters are formed by faces and bodies, and the response patterns distinguish similarly between within-category exemplars in the monkey and the human brain.

Two areas in the body perception network have been the targets of categorical selectivity research. The one reported first was an area at the junction of the middle temporal and middle occipital gyrus, labeled the extrastriate body area (EBA) (Downing et al., 2001). A later added one is in the FG, at least partly overlapping the so-called fusiform face area (FFA) (Kanwisher et al., 1997) and

Table 2
Overview fMRI studies on whole body perception: stimuli, task, stereotactic coordinates for EBA and FBA and experimental results.

	Localizer focus stimuli	Localizer contrast stimuli	Experimental stimuli	experimental task (localizer task)	Tal coordinates	Main experimental results in EBA/FG
Downing et al.,2001				(1-back repetition detection)	l_ EBA: -50, -69, 11 r_ EBA: 50, -69, 4	
Grossman and Blake, 2002			Biological motion, scrambled motion, whole body motion	1-back repetition detection (1-back repetition detection)	l_EBA: -39, -70, 14 r_EBA: 41, -66, 11	EBA not differentially active when observing static headless bodies, dynamic whole bodies (with faces) and faces. EBA not differentially active when observing biological motion compared to scrambled motion.
Hadjikhani and de Gelder, 2003			fearful vs instrumental	Passive viewing	l_ FBA: -34, -55, -13 r_ FBA: 35, -55, -14	FFA more activated by observing fearful bodies than instrumental bodies
de Gelder et al., 2004			fearful vs instrumental	Passive viewing	l_ FBA: -32, -51, -14 r_ FBA: 35, -60, -12	FG more activated by observing fearful bodies than instrumental bodies
Chan et al., 2004	Bodies	Faces, tools and scenes	egocentric vs allocentric body parts	1-back repetition detection (1-back repetition detection)	l_ EBA:-45,-73, 4 r_ EBA: 46, -69, 1	Right EBA (not left EBA) more activated by observing allocentric body parts than egocentric body parts. No modulation by self vs other body parts
Astafiev et al., 2004				Visually guided self generation of finger movement (1-back repetition detection)	l_ EBA: -45, -65, 12 r_ EBA: 42, -58, 13	EBA activated by self-generated finger movements.

Cox et al., 2004				1-back repetition detection		FFA only activated by observing bodies with spatially congruent degraded face
Wheaton et al., 2004			Faces hands legs [1]	Passive viewing	r_FBA: 40, -57, -20 [2]	FG more activated by observing dynamic than static legs (not hands) [3]
Sakreida et al., 2005			fingers, mouth, knee, ankle, elbow, wrist, trunk, and shoulder [4]	Motion acceleration monitorring	l_EBA: -37, -73, 14 r_EBA: 41, -70, 9 [5] l_EBA: -38, -76, 17 r_EBA: 40, -64, 18 [6]	EBA more activated when viewing motion of proximal body parts than distal body parts. EBA more activated when viewing motion of axial body parts than proximal and distal body parts.
Peelen and Downing, 2005a	Headless bodies	Faces, tools and scenes		Visually guided self generation of finger movement	l_EBA: -45, -74, -3 r_EBA: 48, -68, 0	EBA activated by self-generated finger movements. Body selectivity in EBA not correlated with self generated movement response
Peelen and Downing, 2005b			Stick bodies vs control	1-back repetition detection (1-back repetition detection)	r_EBA: 45, -65, 2 r_FBA: 40, -43, -17	FBA and FFA show partial overlap. EBA and FBA, but not FFA more activated by observing stick figure bodies than scrambled controls.
Peelen and Downing, 2005c				(1-back repetition Detection)	l_EBA: -43, -72, -2 r_EBA: 46, -70, -1	Between and within session functional localization reproducibility estimate for EBA
Schwarzlose et al., 2005				(1-back repetition Detection)	FBA [No coordinates given]	FBA partly overlaps with FFA. Higher body selectivity in FBA at higher spatial scanning resolution. Non-overlapping FBA voxels show no preference for faces.

de Gelder and Hadjikhani, 2006			Happy vs instrumental			EBA and FBA not differentially activated for observing happy and instrumental bodies presented in the blind field of a hemianope patient.
Downing et al., 2006a		Heterogeneous set of objects (only few presented here)		Passive Viewing	l_ EBA: –45,–69, 4 r_ EBA: 45, –67, 5	r_EBA more activated by bodies than any other category l_ EBA shows similar activation for bodies and birds
Downing et al., 2006b	Headless bodies	Faces, tools and scenes	Incongruent vs congruent	passive viewing (1-back repetition detection)	r_ EBA: 48, -70, 0 r_ FBA: 41, -43, -19	EBA more activated by observing video frames of different actions than when observing successive video frames of a single action
Peelen et al., 2006	Headless bodies	For EBA: Faces, tools and scenes For FBA: Tools	Biological motion vs scrambled motion	passive viewing (1-back repetition detection)	l_ EBA: -45, -74, -1 r_ EBA: 48, -70, 1 r_ FBA: 41, -45, -19	EBA and FBA sensitivity to bodies correlates with sensitivity to biological motion
Morris et al., 2006			background body only face only body-face	Passive viewing	l_EBA: -42, -80, 12 r_EBA: 54, -79, 12	EBA less activated when a face is visible. FG more activated when observing bodies with faces than bodies only or faces only.
Saxe et al., 2006	Headless bodies and body parts	Objects and object parts	Egocentric vs Allocentric body parts	1-back repetition Detection (passive viewing)	l_EBA: -45, -71, 7 r_EBA: 55, -65, 7	Right EBA (not left EBA) more activated by observing allocentric body parts than egocentric body parts.

Spiridon et al., 2006	Body parts	Man-made objects or food			Ant. l_EBA: -58, -70, 8 Post. l_EBA: -63, -80, 24 Ant. r_EBA: 32, -66, -2 Post. r_EBA: 32, -75, 6	FFA not differentially activated when observing faces and body parts
Grosbras and Paus, 2006			Neutral hands angry hands Neutral face angry face control [4]	Passive viewing	l_EBA: -51, -64, 5 r_EBA: 48, -63, 5 l_FBA: -41, -53, -12 r_FBA: 43, -49, -12 [7]	Right FG not differentially activated when observing neutral hands and neutral faces. Left FG more activated when observing neutral hands than neutral faces. EBA activated when observing neutral and angry faces.
Grezes et al., 2007			neutral fearful scramble [1]	Oddball detection (inverted stimulus)	l_EBA: −44, −79, 8 r_EBA: 51, −69, 9 l_FBA: −40, −55, −12 r_FBA: 44, −51, −16	EBA more activated when observing dynamic than static bodies. Right EBA more activated when observing fearful than neutral bodies. FBA more activated when observing static than dynamic bodies
Peelen et al., 2007	Headless bodies	Tools	Emotional body expressions [1]	emotion intensity rating (1-back repetition detection)	l_EBA: -47, -71, 3 r_EBA: 48, -66, 3 r_FBA: 39, -44, -16	EBA and FBA modulated by emotion
Taylor et al., 2007	Headless bodies & body parts	Chairs & object parts	Increasing body amount vs Increasing object amount 	1-back repetition detection (1-back repetition detection)	l_EBA: -47, -71, 0 r_EBA: 49, -65, 4 r_FBA: 38, -41, -17	Increasing activation in EBA with increasing body amount. No gradual increase in FBA
Downing et al., 2007				1-back repetition detection	l_EBA (whole body): -51, -68, 3 r_EBA (whole body): 51, -67, 3 l_EBA (body parts): -48, -67, 6 r_EBA (body parts): 48, -70, 3	
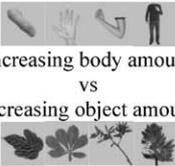
Pichon *et al.*, 2008			neutral scramble / anger [1]	Odball detection (inverted stimulus)	l_ EBA: -44, -83, 4 r_ EBA: 50, -74, 4 l_ FBA: -40, -42, -16 r_ FBA: 42, -50, 1	EBA and FBA more activated when observing dynamic than static bodies. EBA and FBA more activated when observing angry than neutral bodies.
Van den Stock *et al.*, 2008			fearful happy instrumental vs	Oddball detection (chair)	r_ EBA: 45, -63, 4 r_ FBA: 44, -40, -15	EBA of developmental prosopagnosics more activated when observing neutral faces than control subjects.
Lamm and Decety, 2008	Headless bodies (from Downing, 2001)	Chairs	vs intact body part / pain inflicted body part	Evaluation of amount of pain infliction (1-back repetition detection)	l_ EBA: -53 -65 12 r_ EBA: 53, -65, 11	EBA not differentially activated when observing pain infliction on perceived body parts than unharmed body parts.
van de Riet *et al.*, 2009			fearful happy instrumental vs fearful happy neutral	Emotion categorization	l_ EBA: -50, -72, 7 r_ EBA: 53, -64, 9	EBA is not differentially activated when observing fearful or happy bodies than instrumental bodies. FG more activated by bodies than by faces and more by happy bodies.
Hadjikhani *et al.*, 2009			vs fearful instrumental	Passive viewing		FG more activated when observing fearful bodies than instrumental bodies in normals. No differential activation in FG for fearful vs instrumental bodies in ASD
Hodzic *et al.*, 2009	Headless bodies in dark bathing suit	Neutral objects	Bodies in bathing clothes, including participants own bodies	Recognition of own body (1-back repetition detection)	l_ EBA: -43, -73, -7 r_ EBA: 42, -63, 10 r_ FBA: 38, -46, -13	FBA and left EBA more activated when observing self vs other body parts.
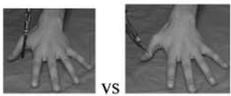
Peelen et al., 2009	Headless bodies (Peelen and Downing, 2005a)	Scenes and tools (Peelen and Downing, 2005a)	dynamic emotional body expressions (Peelen et al., 2007)	emotion intensity rating (1-back repetition detection)	l_EBA: -48, -67, -8 r_EBA: 39, -76, 7 r_FBA: 42, -49, -20	Right FBA and EBA in an acquired prosopagnosic show no emotional modulation.
Kret et al. (submitted)			 Instrumental angry / fearful vs Neutral / fearful angry	Oddball detection	l_EBA: -50, -72, 7 r_EBA: 50, -72, 7	FG more activated by bodies than by faces. EBA more activated when observing dynamic fear and anger expressions than neutral expressions
Sinke et al., (2009)			 threatening teasing scramble (4)	Emotion categorization & color categorization	l_EBA: -46, -68, 4 r_EBA: 45, -65, 1 l_FBA: -39, -44, -15 r_FBA: 37, -43, -13	EBA and FBA more activated when observing threatening vs teasing human interactions. EBA and FBA more activated when performing interaction categorization than rapid dot detection
Van den Stock et al., (in prep)				(1-back repetition detection)	l_EBA: -47, -65, 16 r_EBA: 49, -65, 7 l_FBA: -39, -42, -19 r_FBA: 40, -41, -12	

ASD = autism spectrum disorder; Ant = anterior; Post = posterior; l_EBA = left EBA; r_EBA = right EBA; l_FBA = left FBA; r_FBA = right FBA. All stimuli are static unless stated otherwise: (1) dynamic and static stimuli, (4) dynamic stimuli; (2) coordinates based on comparison of observation of dynamic vs. static legs; (3) study focused on MT/V5, so no conclusions about EBA are available from the study; (5) coordinates based on comparison of observation of proximal motion vs. observation of distal motion; (6) coordinates based on comparison of observation of axial motion vs. observation of distal and proximal motion; (7) coordinates based on comparison of observation of neutral hands vs. control.

termed the fusiform body area (FBA) (Peelen and Downing, 2005b) (see Table 2). Note that as the findings about FBA suggest, face and body category representation may be very closely related. It is a reasonable question whether the sight of a body activates face representations and vice versa because it is well known that when shown familiar stimuli presented in an unusual fashion the brain will automatically fill in the missing information. This issue is important for the notion of category specific representation and has not extensively been addressed (but see Cox et al., 2004).

There are only a few fMRI investigations in humans presenting a direct comparison between faces and bodies. In one such study, subjects were scanned while they viewed static images of neutral and emotional (fearful and happy) faces and bodies and categorized the emotion expressed by the stimulus, irrespective of category. When we compared the hemodynamic brain responses of faces vs. bodies (irrespective of emotional expression) we observed that perception of bodies triggers a broad network of brain areas, including areas previously associated with perception of faces, like the FG, STS, and the middle occipital gyrus (van de Riet et al., 2009). Next to these, also the superior occipital gyrus (SOG), the parieto-occipital sulcus (POS) and the intraparietal sulcus responded more to bodies than to faces. Areas more responsive to faces than bodies were restricted to the calcarine sulcus, cerebellum, superior frontal gyrus and anterior cingulate gyrus. Other studies typically focus on the FG and compare areas that respond more to bodies than to objects with areas that respond more to faces than to objects (Peelen and Downing, 2005b; Schwarzlose et al., 2005; Spiridon et al., 2006) rather than a direct comparison between faces and bodies. Using this indirect comparison approach, a previous study by Schwarzlose et al. (2005) with 7 subjects (in 5 of which a right FBA could be defined) found an effect of scanning resolution on the selectivity for either faces or bodies in the FG, with a positive correlation between selectivity and resolution. Their results showed a higher selectivity for faces in the FG, which is compatible with the results of a subsequent study of the same lab (Spiridon et al., 2006), but shows the inverse pattern of our results. This may be related to methodological issues, such as scanning parameters, applied contrasts or the different object categories that were presented.

Other issues hamper a direct comparison of faces and bodies. First, the face is only a part of an object (person), whereas a body (even with the facial area blurred) constitutes a complete object. This may play a role not only when comparing faces with objects, but also when making the indirect comparison: faces vs. objects

compared to bodies vs. objects. Second, perception of faces allows a detailed and fine-grained analysis of the tonus of the complex musculature of the face, whereas bodies are generally covered with clothing, which may conceal important information about muscle tension, especially when dealing with emotional expressions. Also, the presence of clothing implies perception of man-made objects, whereas faces are typically presented in isolation.

5. Emotional modulation of body-selective processing

The studies discussed so far used still images as well as static bodies, i.e. bodies not engaged in any activity nor showing an emotional expression. As the case of faces illustrates, there are now many reports showing that facial expressions trigger activations that are earlier and spatially different from those typically obtained previously with neutral faces. These findings are clearly important because they challenge accepted traditional models of face processing which typically start from structural face encoding and associate this with the, e.g. time window of N170.

Using ERP recordings we found evidence for very fast automatic processing of bodily expressions. Images of fear expressions compared to neutral bodies shown as performing the same action already affected the ERP responses in the earliest stage of visual perception, i.e. the P1 component (van Heijnsbergen et al., 2007). In addition, this component showed sensitivity to emotional congruence of the body and face (Meeren et al., 2005). Using MEG and anatomically realistic distributed source modeling we were able to confirm and extend these first results (Meeren et al., in preparation). Within the first 120 ms after picture onset, bodies expressing fear differentially activated the occipital pole, regions in the anterior temporal lobe, the parieto-occipital sulcus, and the intraparietal sulcus as compared to neutral bodies.

Similar to studies that reported emotional modulation of face specific areas, like FFA and OFA (occipital face area) (e.g. Breiter et al., 1996; Vuilleumier et al., 2001; van de Riet et al., 2009), effects of emotional information on activation levels of body areas in the brain have been investigated. The first study addressing this issue focused on the FG and amygdala (AMG) and found an increased activation for fearful bodies compared to instrumental bodies in both areas (Hadjikhani and de Gelder, 2003). This result was very similar to the most frequently observed result for faces and consistent with a connection AMG–FG. In a follow up experiment, we focused on the whole brain and compared the activation of fearful, happy and neutral body expressions (de Gelder et al., 2004). The results confirmed our previous findings, but showed additionally the involvement of motor areas in the perception of emotional body expressions. Similar results were obtained in a direct comparison of neutral and emotional faces and bodies (van de Riet et al., 2009) in which we also observed that emotional bodies activate cortical and subcortical motor related structures, like inferior frontal gyrus (IFG), caudate nucleus and putamen. These motor areas were not active for emotional faces (van de Riet et al., 2009). Results of emotional modulation of EBA are less clear. We did not observe a difference between neutral and emotional bodies using static body images (van de Riet et al., 2009), but our data with dynamic body expressions show clear emotional modulation of EBA (Grèzes et al., 2007; Pichon et al., 2008; Sinke et al., 2009; Kret et al., submitted for publication). Recently, we demonstrated in monkeys, that perceiving body postures of conspecifics communicating threat increases the BOLD signal in a subset of body-sensitive voxels in the STS (de Gelder and Partan, 2009).

6. Static vs. dynamic body perception

All studies discussed so far used static facial and bodily pictures. But in real life, we are confronted with faces and bodies in motion.

Although static body pictures may imply motion, dynamic stimuli contain explicit movement information.

Studies of bodily expressions reported better recognition rates for dynamic than static emotional body stimuli (de Meijer, 1989; Atkinson et al., 2004). Two studies designed to find out specifically what additional information is contributed by the dynamics used 3 s video clips showing a person opening a door in either a neutral, a fearful (Grèzes et al., 2007) or an angry (Pichon et al., 2008) way, and compared them to still snapshots taken from the same video clips. Not surprisingly, the dynamic body expressions vs. the static expressions (irrespective of the emotional content) triggered activity in motor areas (bilateral activations of the premotor cortex (PM)). Emotion processing areas (parietal cortex, STS and FG), but also EBA, were active when comparing the emotional vs. the neutral stimuli, irrespective of whether they were presented in a dynamic or static mode. But the most interesting finding was an interaction between emotion and motion in STS and right PM, with stronger motion-related activation for the actions expressing fear as compared to the neutral actions. Interestingly, STS, PM and parietal cortex were activated during action observation and could be involved in action understanding (Grèzes and Decety, 2001). STS and PM may also be essential for bodily emotion understanding since they seem to represent the emotional action.

A recent fMRI study takes research on body perception one step further by investigating the neurofunctional basis of observing interactions between two people. Sinke et al. (2009) used 3 s video clips in which a male actor tries to grab the handbag of a female in either a threatening way (by which the girl is really frightened) or in a teasing way (as if they know each other). During each movie, three small dots appear each for 40 ms. In one task condition, participants had to categorize the interaction as threatening or teasing, and in the other they had to ignore the bodies while monitoring the randomly appearing dots and categorize their color, this is to try to get their attention away from what really goes on in each situation. This study showed that the right AMG reacts in both cases more to the threatening than teasing movies. When the observer's attention is not explicitly directed to the interaction, this goes together with heightened activation in body-sensitive visual regions in FG, posterior middle temporal gyrus and STS. In line with this activation pattern, participants showed a better behavioral performance during the threatening unattended inter-actions. Furthermore, regions involved in action observation (IFG, temporo-parietal junction (TPJ) and inferior parietal lobe) and preparation (PM, putamen) showed activation for threatening videos, even though the threat is not directed towards the observer.

Following up on the direct comparison of still pictures of faces and bodies by van de Riet et al. (2009) we used dynamic stimuli (Kret et al., submitted for publication) to record female and male participants' hemodynamic brain activity while they observed short video fragments in which female and male actors expressed either fear, anger or neutral signals with the face or body. The AMG was sensitive to all expressions, but significantly more to faces. The areas for processing bodies included FG, EBA and STS. Besides that, we observed activation for threatening body expressions, whether fearful or angry, in EBA, right TPJ and the somatosensory cortex. Whereas studies using static stimuli failed to find evidence for emotion modulation in EBA (de Gelder et al., 2004; van de Riet et al., 2009), dynamic emotional stimuli generally trigger more EBA activity than neutral stimuli (Grèzes et al., 2007; Peelen et al., 2007; Kret et al., submitted for publication). The role of the EBA in emotional processing has not been fully understood yet and it is too early to claim that EBA is specifically sensitive for bodily features and less to the configural representation of a body such as the FG. Moreover, some interesting effects of gender were observed in this area. EBA is more active for bodily than facial expressions,

especially when threatening, even more so when expressed by a male actor and above all when observed by a male participant.

7. Bodies may be processed without attention and visual awareness

There is an extensive literature on implicit (i.e. nonconscious) processing of facial expressions (de Gelder et al., 2001a; Eastwood and Smilek, 2005; Johnson, 2005; Vuilleumier, 2005). Nonconscious processing may occur either because attention is engaged elsewhere, so that the unattended stimulus also goes undetected (Mack et al., 2002), or because conscious vision is directly prevented (Macknik and Livingstone, 1998; Weiskrantz, 2009). Research showing that faces and facial expressions are still processed under conditions of limited attention and awareness has contributed significantly to the view that faces have a special status. Recent evidence now shows a similar situation for bodily expressions. Two separate lines of evidence are provided by studies of neurological patients with attention disorders or with cortical blindness.

Patients with hemi-spatial neglect following lesions to the right parietal cortex fail to report leftward stimuli because of a deficit to orient their attention towards the left (contra-lesional) side of the space (Rafal et al., 1994). It has been previously shown that emotional facial expressions presented to the left side tend to call for attention and are more often detected than neutral faces or objects, therefore partially overcoming the attentional bias (Vuilleumier and Schwartz, 2001; Vuilleumier, 2002; Tamietto et al., 2005). We have replicated this effect by showing that also fearful bodily expressions may automatically summon spatial attention towards the neglected side, even under more stringent testing conditions than those previously used with faces (Tamietto et al., 2007). Some differences, however, may be found in the neural correlates mediating conscious vs. nonconscious processing of faces and bodies in neglect patients. In fact, whereas in the case of faces the involvement of a fronto-limbic system seems relevant to recall attention and restore stimulus awareness (Vuilleumier, 2002), in the case of bodies sensory-motor and interoceptive areas (e.g. insula) appear more critical (Tamietto et al., 2008).

Possibly the clearest example of processing bodily expressions in the absence of stimulus awareness is provided by patients with damage to the visual cortex, because they literally cannot see the stimuli presented to the blind portion of their visual field. It is now established that under appropriate testing conditions such patients may reliably discriminate the visual properties of stimuli whose presence they are unaware (blindsight) (Weiskrantz, 2009). This ability to discriminate the attributes of unseen visual stimuli also extends to their affective valence (affective blindsight) (de Gelder and Tamietto, 2007). The initial reports used facial expressions and affective pictures, with positive results for the former stimuli and negative results for the latter, therefore suggesting a special status for faces in conveying nonconscious emotional information via subcortical pathways (de Gelder et al., 1999, 2001c, 2002, 2005; Anders et al., 2004; Pegna et al., 2005). However, affective blindsight exists also for bodily expressions (de Gelder and Hadjikhani, 2006; Tamietto and de Gelder, 2008; Tamietto et al., 2009a). A comparison with bodies and faces is based on behavioral performance (i.e. response accuracy and latency) (de Gelder et al., 1999, 2001b; Tamietto and de Gelder, 2008), peripheral responses (e.g. expressive or autonomic reactions to the stimuli) (Tamietto et al., 2009a), or neural underpinnings of nonconscious processing (Morris et al., 2001; de Gelder et al., 2002; Anders et al., 2004; Pegna et al., 2005; de Gelder and Hadjikhani, 2006; Tamietto et al., 2009b). Analysis of all these response parameters in patients with affective blindsight indicates that faces and bodies induce highly similar responses. Therefore, the emerging picture shows that

nonconscious processing of emotions is not specific for faces but it is clearly documented also for bodies. This indicates that the two types of stimuli share a common representation, possibly in subcortical structures, such as the superior colliculus and amygdala, responsible for coarse evaluation of the affective relevance of visual stimuli.

Finally, an interesting issue is whether emotional meaning may be extracted nonconsciously from specific parts of the face or body, or whether this requires prior analysis of the overall configuration of the stimuli. There is initial evidence that specific regions of the face, such as the eyes, may be sufficient in conveying the affective information outside visual awareness (Whalen et al., 2004). A recent study recording eye movements has found which specific body parts (hands, arms, legs and the position of the trunk) attract the gaze that varies with the specific emotion displayed. For example, when observing angry bodily expressions, subjects fixate primarily at the hands while for sad expressions they look at the face (Fridin et al., submitted for publication).

8. Learning from lesions

An argument in favor of the higher overall category specificity faces than of bodies may be that of a specialized neurofunctional substrate for faces but not for bodies. We have already reviewed this argument as far as the neurologically intact brain is concerned. But a strong impetus for face and more generally category specificity of neural substrates comes from neuropsychological reports of patients with brain damage acquired in adulthood. There is a well-known neuropsychological deficit related to impaired face recognition, labeled prosopagnosia or face blindness. These patients are impaired in recognizing faces, and very often have no recognition at all of an individual by the face only. Brain damage occurring in the normally developed brain that affects face perception is often localized in occipitotemporal cortex and temporal cortex (FG and IOG) unilaterally or bilaterally. The developmental counterpart of acquired prosopagnosia is also increasingly reported now. There is substantial similarity between acquired and developmental prosopagnosia at the behavioral level but there are many other differences (see de Gelder and Rouw, 2000 for a comparison).

It is important to specify the exact nature of the face disorder and this is still a matter of debate. The short definition of prosopagnosia characterizes it as a deficit in face recognition. But this is too broad and also too a-specific. We are in fact dealing with a deficit that affects recognition of personal identity from the sight of the face. Other dimensions of face information are processed mostly normally, like emotional expression, visual speech or gender. In fact, the reliable means of defining the typical face deficit of prosopagnosics is by establishing that there exists dissociation between the different dimensions of face perception, some of which are impaired while others are intact. In addition, a dissociation must be established requiring evidence that the perception and recognition impairment is not present for non-face stimuli. But there are to date only very few cases of pure prosopagnosia, where the perception and recognition deficit is restricted to the face and does not affect other object categories. To establish the presence of developmental prosopagnosia (DP) the same dimensions of dissociation need to be assessed. Thus when making the parallel argument for 'body blindness' the aspect of body perception, that is impaired vs. the ones that are intact require evidence. These two dimensions of dissociation need to be taken into account. Therefore the equivalent of face deficit in the case of body perception is also likely to consist of one dimension of body perception and recognition.

On the other hand, using body stimuli offers a chance to advance the debate on category specificity of faces. For example,

the behavioral and neurofunctional similarities between perceiving faces and bodies in neurologically intact observers raise the issue how bodies are processed in DP. We investigated perception of emotional and neutral faces and bodies in DPs and normal controls (Van den Stock et al., 2008). The results showed a lower activation for neutral faces in FFA in the DP-group compared to the control group, but there was no difference between both groups for the emotional faces in FFA. We also compared activation of body expressions in face-selective regions and of facial expressions in body-selective regions. Our findings indicate that perceiving neutral faces results in a higher activation of EBA in the DP-group, compared to the control group. Combined with the lower activation in FFA for neutral faces, this increased activation in EBA may indicate an anomalous processing route in the brains of DPs. It may be the case that (neutral) faces are processed in the areas more dominantly dedicated to body perception. On the other hand, we found a higher activation for perceiving bodies in IOG. These combined findings indicate that the neural correlates of perceiving faces and bodies in IOG and EBA show a lower degree of specificity in DP. These results are clearly tentative. Further research is needed to determine whether these differences in face and body processing between DP and controls reflect differences in processing routes or may result from compensation for the face processing deficits of DP.

Recently, a triple dissociation was demonstrated between faces, bodies and objects when different regions of the extrastriate occipital cortex were temporarily inactivated by transcranial magnetic stimulation (TMS) (Pitcher et al., 2009). Stimulating EBA resulted in a selective body-processing deficit, whereas stimulating OFA and LOC (lateral occipital complex) (Malach et al., 1995) resulted in a selective impairment of face and object discrimination, respectively. These findings strongly support a (partly) modular organization of the human brain. But here also an important issue is whether this picture remains the same when functional aspects like, for example the emotional expression are taken into account.

9. Models of body perception

In the last five years a few theoretical models of body perception have been advanced. The first one in de Gelder et al. (2004) was based on the only whole brain fMRI data available at that time and systematized the brain areas that differentially activated to neutral body actions and bodily expressions. It distinguishes between processes involved in low level body detection, on the one hand, and body perception and recognition, on the other, and provides room for contribution of subcortical structures to detection and expression recognition. Integration of those initial results with new information provided by other techniques as well as by lesion studies led to the model in de Gelder (2006) in which body perception is envisaged along three interconnected networks: a predominantly subcortical one sustaining reflexive reactions, a cortical one sustaining visual analysis and reflective action and an interface system of bodily awareness.

Models addressing a more specific range of data provided by studies of neutral still bodies and focussing on the issue of part vs. whole processes in body perception are provided in Taylor et al. (2007), Urgesi et al. (2007) and Hodzic et al. (2009). These models of neutral body perception are reminiscent of the earlier models of face processing in which typically a number of separate stages were distinguished. They tend to be hierarchical and serial and address functional and neural questions about face perception mainly from the vantage point of how recognition of personal identity is achieved. But as convergence grows between the researchers of face recognition in this narrow sense and those working on facial expression recognition a rapprochement is seen

between the two kinds of models. A major impetus for this rapprochement came from findings that facial expressions were perceived "earlier" than encoding of the face structure and that there was residual face processing ability in patients with cortical damage. These findings and others led to extended models of face processing encompassing both early and late processes, both expression and identity (de Gelder and Rouw, 2000; Haxby et al., 2000; Adolphs, 2002; de Gelder et al., 2003) and involving conscious as well as unconscious, cortical but also subcortical structures and detection and recognition routes (de Gelder and Rouw, 2000; de Gelder et al., 2003).

Two sets of results available already about body perception allow us to anticipate that something similar is likely to be needed for bodies and for bodily expressions. One is that bodily expressions seem to trigger earlier activation in striate and extrastriate visual cortex, anterior temporal areas, but also more dorsal structures like parieto-occipital sulcus and intraparietal sulcus (Meeren et al., in preparation). Consistent with this and similar to findings about facial expressions, bodily expressions already show an emotional action trigger at the P1 component in the 100–120 window (Meeren et al., 2005; van Heijnsbergen et al., 2007), before the structural encoding of the stimulus has taken place. Importantly, those early activations testify for configural processing of the body stimulus as reflected in the fact that there is an early inversion effect (Meeren et al., 2008). The second important set of findings is the existence of residual processing of body stimuli in patients with cortical damage (de Gelder and Hadjikhani, 2006; Tamietto and de Gelder, 2008; Tamietto et al., 2009a) which is again similar to face processing, calling for body perception models that also acknowledge the contribution from subcortical structures which are important for rapid visual analysis and reactive behavior.

Of course, all models are tentative till more research is available. As our overview illustrates, a focus on isolated, single function areas is difficult to maintain when issues of control conditions and task demands are acknowledged. For example, when considering the function of EBA in itself, one issue is puzzling though. Urgesi et al. (2007) as well as Taylor et al. (2007) and Hodzic et al. (2009) attribute featural but not configural processing to EBA. Yet it emerges from studies of bodily expressions mentioned already (Grèzes et al., 2007; Pichon et al., 2008) that EBA is sensitive to whether there is affective information in the body stimulus. This modulation by emotion may be compatible with EBA as a feature processor, in which case one would need to investigate which specific body part conveys the affective information. Alternatively, EBA does process the configuration of the stimulus after all. This alternative is consistent with our findings that EBA is differentially sensitive to affective information in the body (Grèzes et al., 2007; Pichon et al., 2008) when videos are used. This ambiguity as well as that concerning FG suggests that the role of an area is best investigated in connection with its role in a network.

10. Conclusion

For at least three decades faces occupied the most prominent position on the research agenda of psychologists, neuropsychologists, neurophysiologists and cognitive neuroscientists. The reasons for this situation are diverse. They range from recognition of the evolutionary and communicative importance of the face to conceptual and philosophical considerations about the need for a modular organization of the brain reflected in specialized perceptual abilities. Modular theorists have typically used the case of language and that of face perception as the clearest examples. In this paper we have tried to put current findings in perspective without however pushing them in the framework of

the traditional question of modularity. We have argued that a number of different dimensions need to be considered when comparing the behavioral, neurofunctional and neuropsychological basis of faces and bodies. The debate is open, but it would be a pity to limit it to the traditional questions and debates about specilized modules and categorical representation in the brain. When viewed in a broader perspective, faces and bodies are comparable because they both convey information that is essential for social interaction. Yet they each fulfill this role in a different way. It seems likely that faces are used for fine-grained analysis of communication intention and possibly also convey a broader range of subtle emotions in a setting of close-by person to person. In contrast, while body language is still important for close-by interaction, bodily expressions allow for appraisal of action intention and emotions over larger distances. These differences are lost when one focuses only on representation issues.

Acknowledgements

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