

Neural Integration in Body Perception

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Abstract

■ The perception of other people is instrumental in guiding social interactions. For example, the appearance of the human body cues a wide range of inferences regarding sex, age, health, and personality, as well as emotional state and intentions, which influence social behavior. To date, most neuroscience research on body perception has aimed to characterize the functional contribution of segregated patches of cortex in the ventral visual stream. In light of the growing prominence of network architectures in neuroscience, the current article reviews neuroimaging studies that measure functional integration between different brain regions during body perception. The review demonstrates that body perception is not restricted to processing in the ventral

visual stream but instead reflects a functional alliance between the ventral visual stream and extended neural systems associated with action perception, executive functions, and theory of mind. Overall, these findings demonstrate how body percepts are constructed through interactions in distributed brain networks and underscore that functional segregation and integration should be considered together when formulating neurocognitive theories of body perception. Insight from such an updated model of body perception generalizes to inform the organizational structure of social perception and cognition more generally and also informs disorders of body image, such as anorexia nervosa, which may rely on atypical integration of body-related information. ■

INTRODUCTION

The appearance of the human body provides a rich source of social information. Bodies signal cues to an observed individual's sex, age, health, and personality, as well as his or her emotional states and intentions. Such signals are important for social interactions, as they guide human behavior in terms of approach/avoidance tendencies, mate selection, and cooperation. Given their instrumental influence on daily life, research has aimed to identify the neurobiological mechanisms by which such signals are detected, processed, and utilized (Frith & Frith, 2010).

Research investigating the perception of other people—social perception—has been dominated by the study of faces (Jack & Schyns, 2017; Duchaine & Yovel, 2015; Kanwisher, 2010; Haxby, Hoffman, & Gobbini, 2000; Bruce & Young, 1986). Faces play a central role in social interactions, and as a consequence, face perception research has provided valuable insights. However, bodies also cue a range of information that is exploited during social interactions (de Gelder et al., 2010), which, at times, faces conceal (Aviezer, Trope, & Todorov, 2012). Therefore, if a core aim of social perception research is to understand how we read and navigate social signals in the real world, bodies are also a vitally important cue to study. Moreover, bodies, like faces, can be studied as a model system to investigate the cognitive and neural processes that underpin social perception.

The majority of neuroscience research on body perception has focused on understanding the role of segregated patches of cortex in the ventral visual stream (for reviews, see Downing & Peelen, 2011, 2016). This work has identified two regions of ventral temporal cortex (fusiform body area [FBA], extrastriate body area [EBA]) that respond more robustly to bodies than other classes of stimuli, such as houses and chairs. FBA and EBA, therefore, are said to show category selectivity for bodies. Although many functional claims have been made for the role of these two regions, the majority of evidence suggests that these regions primarily process body shape and posture (Downing & Peelen, 2011).

Complicated mental processes, such as those underpinning aspects of social perception, are unlikely to rely solely on segregated patches of cortex acting alone, however (Ramsey, van Schie, & Cross, 2011; Kanwisher, 2010). Rather, mental processes are likely to involve the integration of interacting signals that span across distributed neural networks (Bullmore & Sporns, 2009; Fuster, 1997; Mesulam, 1990). Indeed, two cornerstones of brain function are functional segregation and functional integration (Park & Friston, 2013). Functional segregation is characterized by information processing that is carried out by functionally related brain regions that are arranged in modules,¹ whereas functional integration involves the exchange of signals across a distributed set of such brain networks or modules (Park & Friston, 2013; Sporns, 2013). Given the range and complexity of social information that bodies are associated with, responses in ventral temporal cortex are likely to be a combined product of

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local, as well as distributed, processing functions (Sporns, 2013). To date, however, little is known about the role of functional integration in body perception.

The main aim of the current article is to review neuroimaging evidence for functional integration in body perception and consider the implications of functional integration research for understanding the neural bases of social perception. The article is organized in four parts. First, to provide a relevant context, a brief review of evidence for functional segregation in body perception is provided. Second, lines of evidence from fMRI studies that have investigated functional integration in body perception are reviewed. These studies show that brain circuits in ventral temporal cortex and those in extended networks associated with action perception, executive functions, and theory of mind integrate information during body perception. Together, the first two sections of the article suggest that, by considering functional segregation and integration together, we will have a more complete understanding of the neural systems that support body perception. Third, the implications of such an updated neurocognitive model of body perception for understanding social perception and cognition more generally, as well as disorders of body image, are discussed. Finally, future directions that embrace network science approaches to understanding social perception are outlined.

FUNCTIONAL SEGREGATION IN BODY PERCEPTION

A primary neuroimaging method for identifying category selectivity in the human brain has been to adopt a func-

tional ROI approach (Kanwisher, 2010, 2017). The functional ROI approach typically uses univariate methods for comparing responses across different categories of stimuli. First, ROIs are identified based on functional data using a “localizer” scan, before the response in these regions is interrogated using separate task data. This approach has identified two body-selective regions in ventral temporal cortex (FBA and EBA), which respond to bodies more than other object categories such as houses and chairs (Figure 1A; Zhan, Goebel, & de Gelder, 2018; Peelen & Downing, 2005; Downing, Jiang, Shuman, & Kanwisher, 2001; for a review, see Downing & Peelen, 2011). Functional divisions have also been identified within this body circuit with FBA showing greater sensitivity to whole bodies and EBA showing greater sensitivity to body parts (Taylor, Wiggett, & Downing, 2007).

Although there is clear evidence for body shape and posture processing in FBA and EBA, more elaborate cognitive processes have also been ascribed to these regions including identity, emotion, and action-related processes (Downing & Peelen, 2011). However, there is less convincing evidence for these more elaborate representations in ventral temporal regions (Downing & Peelen, 2011). Like the majority of brain networks, responses in ventral temporal cortex are likely to index a local processing function as well as an exchange of signals within a wider neural network (Sporns, 2013). As such, claims based on univariate responses in EBA and FBA may reflect the exchange of signals with wider brain networks in addition to local processes (Park & Friston, 2013). This is especially the case for more elaborate representations associated with social cognition, which have been shown to recruit a widely distributed neural architecture (Frith & Frith, 2010; Figure 1B). Evidence

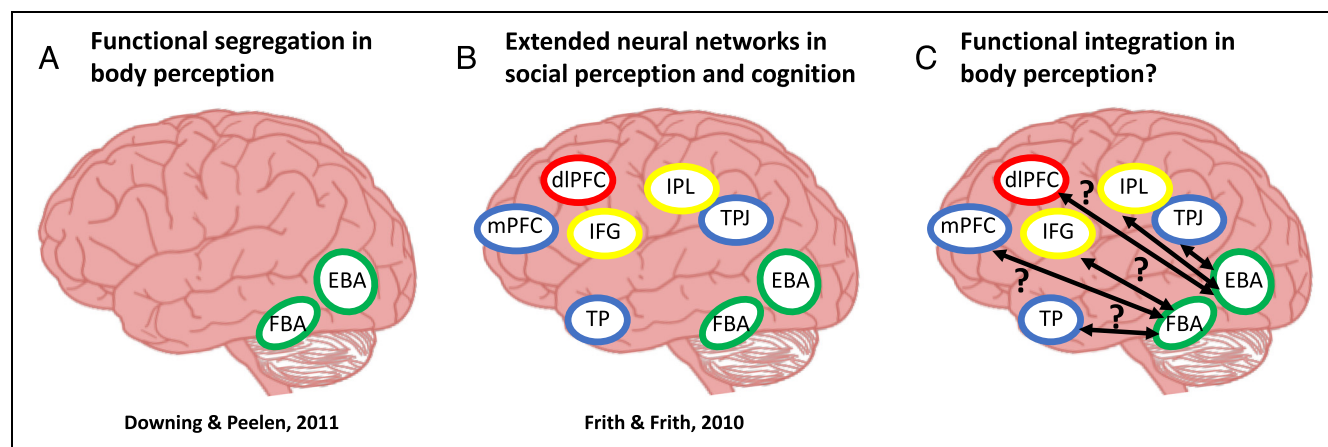


Figure 1. Functional segregation in body perception and social cognition. The majority of research investigating body perception (A) and social cognition (B) has focused on understanding the role of functional segregation. Functional segregation is characterized by information processing that is carried out by functionally related brain regions that are arranged in modules. Less body perception research has investigated the role of functional integration between brain networks (C). Functional integration is characterized by the exchange of signals across a distributed set of brain networks or modules. Abbreviations: mPFC = medial pFC; TP = temporal pole; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; dIPFC = dorsolateral pFC. Color scheme: green = body-selective cortex; blue = theory-of-mind network; yellow = mirror neuron system; red = executive control circuit.

for interactions between body-selective areas in ventral temporal cortex and wider networks associated with social perception and cognition are reviewed in the next section.

FUNCTIONAL INTEGRATION IN BODY PERCEPTION

Complex mental processes, such as those subserving social perception and social inference, are unlikely to rely on a narrow use of neural tissue that is restricted to ventral temporal cortex (Duchaine & Yovel, 2015; Ramsey et al., 2011; Kanwisher, 2010; de Gelder, 2006; Haxby et al., 2000). Models of emotional body perception, for example, are based on a distributed and interacting set of brain networks (de Gelder, de Borst, & Watson, 2015; de Gelder, 2006). To measure network connectivity, neuroimaging methods have been developed that enable interactions between distinct anatomical or functional regions to be estimated (Friston, 2011). Although many connectivity studies measure resting state activity (Greicius, Krasnow, Reiss, & Menon, 2003), other studies measure how connectivity changes as a function of the experimental condition, such as the type of task or stimulus (Friston, 2011; Friston et al., 1997).

Such task-based functional connectivity approaches substantially extend univariate approaches by first identifying functional ROIs using established localizers and then estimating how these networks interact as a function of the task or stimulus set. At least two broad classes of task-based connectivity have been developed: directional and correlational. Directional measures of functional connectivity, such as dynamic causal modeling (DCM) and Granger causality, permit inferences to be drawn regarding the direction of influence of one brain region on another (Friston, 2009). In contrast, purely correlational measures, such as psychophysiological interactions (PPI), are unable to provide an estimate of the direction of influence (McLaren, Ries, Xu, & Johnson, 2012; Friston et al., 1997). Instead, PPI relies on general linear modeling to estimate how correlations between brain regions vary as a function of task demands. Importantly, PPI modeling procedures typically include univariate and PPI regressors within the same model, which means that, for PPI regressors to be of interest, they must explain variance above and beyond that explained by the univariate regressors (McLaren et al., 2012; O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012).

Although it has been proposed that body perception involves a distributed neural architecture that extends beyond ventral temporal cortex (e.g., Ramsey et al., 2011; de Gelder, 2006), fewer than 10 studies have investigated functional integration during body perception using fMRI. Univariate neuroimaging techniques as well as neuropsychology lesion studies show that recognizing emotional body postures relies on a distributed neural

architecture that extends beyond ventral temporal cortex (for reviews, see de Gelder et al., 2015; de Gelder, 2006). However, the lack of functional connectivity studies means that the boundary conditions that govern local processing and distributed processing in body perception remain unclear (Figure 1C). Indeed, neural integration research in body perception has only just begun to identify which neural circuits interact with ventral temporal cortex and in which social contexts. In this section, I focus on studies that have used fMRI and measures of task-based connectivity during body perception. These studies have investigated the relationship between body perception and a range of different topics including identity recognition, action perception, executive control, and theory of mind.

Integration within the Ventral Visual Stream

Ewbank and colleagues (2011) used a repetition suppression design to investigate functional interplay between FBA and EBA during the processing of physical identity. Repetition suppression is observed when a repeat stimulus feature produces a reduced neural response and has been used to test population coding models of perception and cognition (Barron, Garvert, & Behrens, 2016; Grill-Spector, Henson, & Martin, 2006). In Ewbank and colleagues' (2011) study, participants observed body images that varied in size, orientation, and identity. When there was a repeat identity, both FBA and EBA showed a reduced response, thus showing repetition suppression for person identity. In addition, Ewbank and colleagues (2011) used DCM to show that FBA modulated responses in EBA for a repeated compared with a novel identity. This response was invariant to changing size and view of the body. The authors suggest that FBA provides top-down control over the response in EBA. Such an interpretation is consistent with the view that FBA represents whole bodies (irrespective of size and viewpoint changes) and influences a more granular, body part-specific representation in EBA that is tuned by body size and view (Taylor et al., 2007). Hence, this study shows that body identity processing is not only a product of local responses in FBA and EBA but instead reflects integration between these two nodes (Figure 2A).

Integration between the Ventral Visual Stream and the Action Perception Network

In addition to integration between EBA and FBA, other studies have shown that body patches interact with wider neural networks associated with action perception, executive functions, and theory of mind. In terms of action perception, Zimmermann, Toni, and de Lange (2013) showed that body posture modulates the perception of another's action goals. The authors found that, when a participant's body posture matches an observed action,

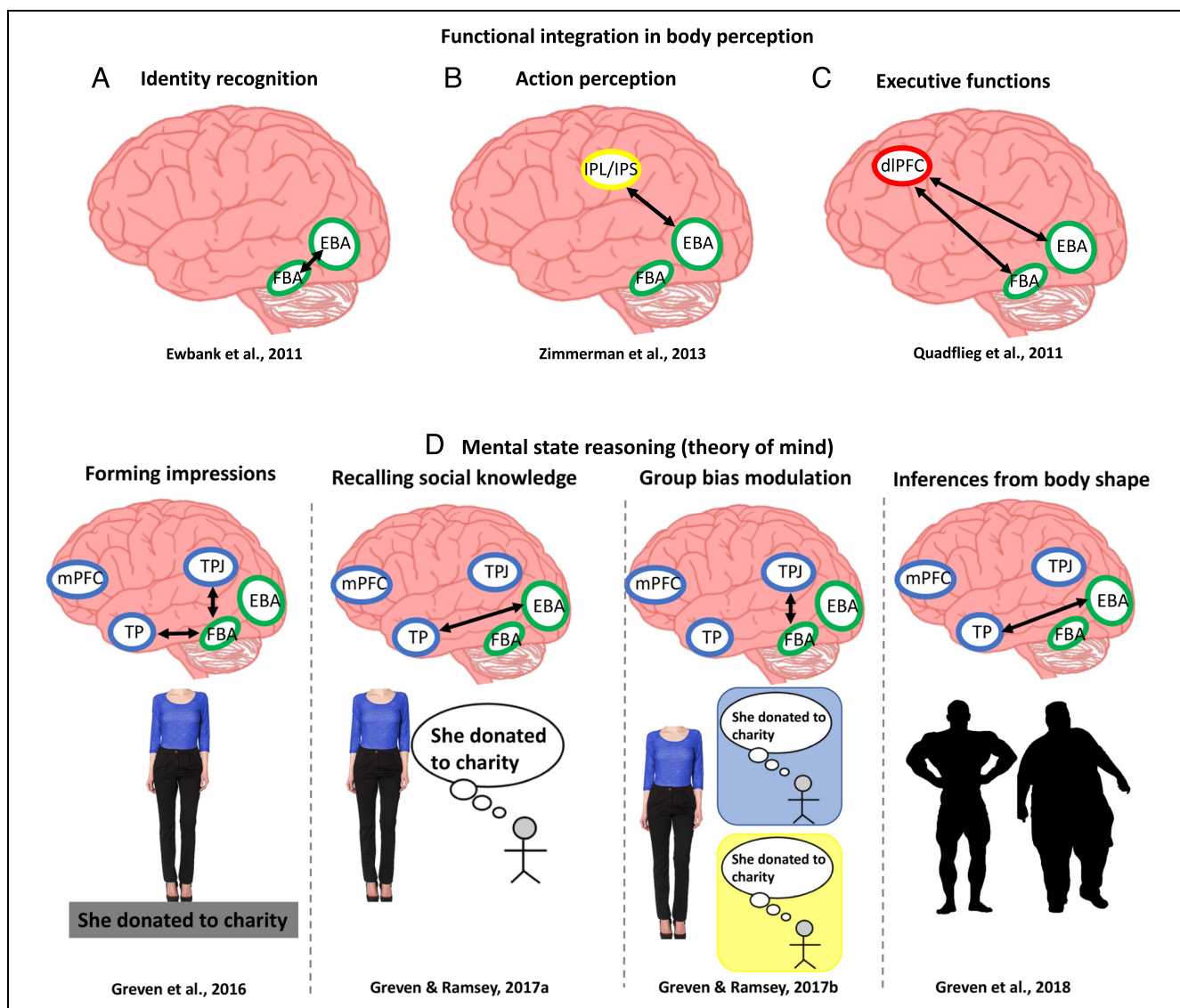


Figure 2. Functional integration in body perception. A summary of fMRI studies that have investigated functional integration in body perception. These studies have used measures of functional connectivity to estimate links within the ventral visual stream during identity processing (A) as well as between the ventral visual stream and networks associated with action perception (B), executive functions (C), and theory of mind (D). Abbreviations and color scheme as Figure 1.

the prediction of another's action goal is facilitated. In support of this goal ascription process, the intraparietal sulcus was engaged more when there was a mismatch between the participant's body posture and the observed action goal posture. In addition, using PPI, the response in intraparietal sulcus correlated with EBA as a function of action frequency: observing low-frequency actions increased coupling. The authors interpret the neuroimaging results within a predictive framework, under the assumption that body perception signals in ventral temporal cortex contribute to a prediction of a person's likely goal. The goals associated with more frequently observed actions are less surprising and result in lower prediction error. By contrast, less frequent actions produce a higher prediction error, and thus, a greater signal

exchange between intraparietal sulcus and EBA is required to update the goal estimate (Figure 2B). These results, therefore, document a link between ventral temporal cortex and brain regions associated with the perception of action goals.

Integration between the Ventral Visual Stream and Executive Functions

Perception in general, whether of objects, scenes, or people, has been shown to involve interplay between the visual stream and neural systems associated with executive functions (Baldauf & Desimone, 2014; Bar, 2004). Executive functions are a set of mental processes that are needed to accomplish difficult tasks, when relying on

automated processes would be ineffective (Diamond, 2013). Using a paradigm that manipulated the presence of sex-based stereotypes, processes associated with body perception have been shown to have a similar interactive relationship with executive functions (Quadflieg et al., 2011). When we meet other people, we categorize them into social groups based on many factors, such as sex, age, profession, and race. We also hold stereotyped expectations for such social groups, which influence social interactions (Macrae & Quadflieg, 2010; Fiske & Neuberg, 1990; Brewer, 1988). For instance, we typically expect nurses to be female and courtroom judges to be male. In some instances, however, individuals violate stereotypical expectations (e.g., a male nurse). When performing sex judgments of others in situations that violate sex-based stereotypes compared with those that conform, Quadflieg et al. (2011) showed increased coupling between dorsolateral pFC and body-selective patches in the ventral visual stream. The authors suggest that dorsolateral pFC modulates visual processing of object categories, in this case bodies, to override the initial expectation based on bodies and to modulate the formation person percepts in the brain (Figure 2C).

Integration between the Ventral Visual Stream and the Theory-of-Mind Network

Theory of mind is the attribution of mental states, such as beliefs, desires, and attitudes, to others and has been consistently associated with the engagement of medial pFC, TPJ, temporal poles, and precuneus (Van Overwalle, 2009; Saxe & Kanwisher, 2003; Frith & Frith, 1999). The theory-of-mind network responds to a variety of tasks involving mental state attribution and social inferences (Van Overwalle, 2009) and can be reliably identified with a short belief reasoning functional localizer during fMRI (Dodell-Feder, Koster-Hale, Bedny, & Saxe, 2011).

Using body perception and theory-of-mind localizers, a series of studies has investigated the relationship between body-selective patches in ventral temporal cortex and the theory-of-mind network during body perception (Figure 2D; Greven, Downing, & Ramsey, 2016, 2018; Greven & Ramsey, 2017a, 2017b). Each study investigated a distinct component of social information processing during body perception, including the formation (Greven et al., 2016) and recall (Greven & Ramsey, 2017a) of impressions, the impact of group bias on body perception (Greven & Ramsey, 2017b), as well as person inferences that are based on body shape alone (Greven et al., 2018). The broad hypothesis across these experiments was the same: Social information processing during body perception will not be restricted to univariate responses in segregated networks but will also be indexed by integration between body-selective and theory-of-mind networks.

The first study investigated the formation of impressions during body perception (Greven et al., 2016). In a

2 × 2 factorial design, bodies or names were shown to participants alongside a short statement that described behaviors that cued trait-based or neutral judgements (Figure 2D). For example, the statement “She gave money to charity” cues a trait-based inference (e.g., selfless, generous), much more than a trait-neutral statement such as “She sharpened her pencil.” Therefore, the type of inference (trait-based, neutral) and the social target (body, name) were manipulated, and participants were asked to form an impression of the person. Prior work had demonstrated that, compared with neutral statements, trait-based inferences engage the theory-of-mind network (Ma, Vandekerckhove, Van Overwalle, Seurinck, & Fias, 2011; Mitchell, Cloutier, Banaji, & Macrae, 2006). Using PPI, Greven and colleagues (2016) showed that FBA showed stronger functional coupling with TPJ and temporal poles when participants formed an impression of a body compared with when they formed similar impressions based on a person’s name. This suggests that, when forming impressions of others, functional connectivity between FBA and nodes in the theory-of-mind network are tuned to specific types of social information (bodies more than names; trait inferences more than neutral judgements).

Although first impressions are common, much of our daily lives involve interactions with familiar people (e.g., friends, family, and colleagues). As such, we have a rich set of stored person associations, which we rely upon to guide social exchanges. To assess recall of social knowledge that is prompted by body perception, in a subsequent study Greven and Ramsey (2017a) trained participants before scanning to associate different bodies with trait-based or neutral information. During scanning, participants viewed the same bodies and were asked to form an impression of the individual. PPI analyses showed that perceiving bodies that prompted the recall of social knowledge compared with bodies associated with neutral knowledge engaged more functional coupling between EBA and the temporal poles. These results may suggest that the detection of body parts in EBA triggers an exchange of signals with a node in the theory-of-mind network that has consistently been associated with the development of person knowledge (Olson, McCoy, Klobusicky, & Ross, 2013). One possible interpretation of this result is that once identity is established based on body shape and posture cues, there is a relatively rapid exchange with a nonvisual person knowledge representation in the temporal poles.

In addition to stored knowledge regarding trait-based character, we readily recognize others as being part of an ingroup or outgroup based on factors such as sex, profession, race, and age. Such group biases are prevalent in social perception and cognition, and we typically perceive ingroup members more favorably than outgroup members (Brewer, 1999; Allport, 1954). We are also more likely to remember positive information about ingroup members and more negative information about

outgroup members (Fyock & Stangor, 1994). In terms of neural circuits, a distributed set of brain networks are sensitive to group biases, which span visual, affective, and cognitive systems (Amodio, 2014; Molenberghs, 2013). However, little is known regarding functional connectivity between these neural circuits during group bias modulation of person perception. Greven and Ramsey (2017b) used a minimal group manipulation (Tajfel, Billig, Bundy, & Flament, 1971), whereby participants were randomly assigned to a “blue” or “yellow” team and given a long-sleeved t-shirt to wear, which matched their team color. Participants were subsequently shown images of ingroup and outgroup members (i.e., those wearing blue or yellow t-shirts), who were previously associated with positive or negative social information. PPI results showed greater coupling between FBA and TPJ for bias-consistent (ingroup-positive and outgroup-negative) than inconsistent pairings. These results suggest that coupling between the ventral visual stream and the theory-of-mind network is tuned to social knowledge and social group pairings. Indeed, interactions between networks is not driven by main effects of group or valence but instead reflects the combination of the two types of information (ingroup, good; outgroup, bad).

Impressions are not only formed based on explicit knowledge of behavior; impressions are also formed based on physical shape alone. For example, body shape and posture cue inferences regarding emotional state, personality, and health (de Gelder et al., 2010; Puhl & Heuer, 2009; Sell et al., 2009; Borkenau & Liebler, 1992). Using silhouette images of bodies, which emphasize body shape and posture cues, Greven and colleagues (2018) performed two fMRI experiments that investigated the neural bases of inferences that are drawn from body shape alone. Before scanning, three behavioral experiments showed that different body types (obese, muscular) were judged differently on dimensions of personality and health compared with slim bodies. Obese bodies were rated as less extraverted, conscientious, and healthy, whereas muscular bodies were rated as more extraverted and healthy but less agreeable. These results show that social inferences of slim bodies are more neutral (i.e., closer to the middle of the rating scale) when evaluating personality and health than muscular and obese bodies. This does not imply an absence of social inferences for slim individuals, just that inferences are less extreme. In other words, social inferences are made for all body types, and only the content of these inferences varies based on the physical attributes of the bodies. As part of the same study, two subsequent fMRI experiments used the same stimuli but varied the task. The first experiment used a 1-back recognition task and showed no evidence for differential engagement of body or theory-of-mind networks and no coupling between body and theory-of-mind networks. In the second experiment, which required participants to form an impression of the person, evidence emerged for functional coupling

between EBA and the temporal poles, but it was a relatively weak effect. There was, however, clearer evidence for differential engagement of segregated neural circuits: the Muscular > Slim contrast engaged EBA and FBA, whereas the Obese > Slim contrast engaged medial pFC and temporal poles. These results suggest that there is a division of labor between body and theory-of-mind networks when forming an impression based on body shape.

Together, this series of four fMRI studies shows that different dimensions of body perception involve functional interplay between body and theory-of-mind networks. These dimensions include (1) stage of social knowledge acquisition (formation vs. recall), (2) the form of social knowledge (written description vs. body shape), (3) identity of the social target (ingroup vs. outgroup), and (4) intentionality of social inference (unintentional vs. intentional). Considering the results of these studies together suggests that the ventral visual stream and the theory-of-mind network do not act in isolation during body perception but instead exchange signals across multiple social information processing dimensions.

Furthermore, the results permit speculation on a possible division of labor in functional network organization. Forming impressions of another person’s character and tagging such information to body shape is associated with links between FBA and the theory-of-mind network, including the temporal poles and TPJ (Greven et al., 2016). It is possible that developing a richer representation of a person to include nonvisual information (i.e., impressions of trait-based character) involves exchange between FBA and temporal poles, which is consistent with the role of TP in stored person knowledge (Olson et al., 2013) and FBA in a representation of whole bodies (Taylor et al., 2007). It is also consistent with recent work in the domain of face perception, whereby links between the ventral visual stream and temporal poles have been demonstrated to underpin the retrieval of social knowledge that is associated with faces (Wang et al., 2017). By contrast, recall of social knowledge that is prompted by body shape involves links between EBA and temporal poles (Greven et al., 2018; Greven & Ramsey, 2017a). One interpretation is that, when bodies cue social inferences, the detection of body parts in EBA (Taylor et al., 2007) triggers an associated representation of stored social knowledge in temporal poles (Olson et al., 2013). This proposal is consistent with theories of impression formation that posit links between representations of facial features and trait knowledge (Over & Cook, 2018). However, the possibility that networks can be fractionated into functionally distinct partitions remains speculative at the moment. Indeed, models of neural integration between the ventral visual stream and the theory-of-mind network are only just beginning to be formulated, and it will be important for future work to directly test these predictions using a range of methods (see Limitations and Future Directions section).

Summary

In summary, evidence is emerging that different dimensions of body perception involve functional interplay within the ventral visual stream, as well as between the ventral visual stream and neural networks associated with action perception, executive functions, and theory of mind (Figure 2). These results demonstrate that the ventral visual stream does not act alone in body perception but instead forms functional connections with distributed neural networks that span anterior temporal, frontal, and parietal cortices. Next, implications for neurocognitive models of body perception are outlined.

IMPLICATIONS

The primary implication of the reviewed evidence is that body percepts are constructed through relationships between distributed and interacting neural networks. Indeed, links between the visual stream and extended systems are suggestive that information processing in the visual stream is not sufficient to perceive the outside environment (Sterzer, Kleinschmidt, & Rees, 2009; Gilbert & Sigman, 2007). A consequence of this suggestion for neuroimaging research in general is that focusing on segregation alone will produce skewed models of mental processes that are biased toward a segregationist structure and underestimate complexity. This is not to suggest that understanding functional segregation holds no value in social perception. Rather, these results underscore that, to understand complex mental processes, functional segregation and integration need to be considered in partnership (Sporns, 2013). Indeed, fMRI studies that only use univariate approaches must keep in mind that responses may not only reflect a local, segregated function, but also an integrative function.

Studying the perception of bodies, like faces, scenes, words, and tools, is one way to understand organizing principles of human brain function. Here we extend this understanding to show how functionally segregated modules connect to form functionally interacting networks during body perception. Therefore, the reviewed research uses body perception as a model system to investigate mechanisms of social perception, as well as a means to study network models of human brain function more generally. Consequently, the results hold the potential to inform other research domains that also rely on distributed but interacting modules, such as face perception (e.g., Duchaine & Yovel, 2015), object perception (Bar, 2004), and memory (Cabeza & Moscovitch, 2013). For example, similarities are likely to exist between face and body perception (de Gelder et al., 2010), which means core principles from the findings reported here may readily apply to face perception. Relatedly, theories of impression formation, which specify links between the acquisition of trait knowledge and the representation of facial features (Over & Cook,

2018), could be informed by the work reviewed here on links between systems associated with body shape perception and theory of mind. As a further example, functional structures in the domains of memory (Cabeza & Moscovitch, 2013) and object perception (Bar, 2004) involve links between domain-specific and domain-general systems, a picture that also emerges in the body perception research reviewed here. As such, by comparing different information processing domains, common and distinct organizing principles of brain function can emerge, which may lead to new hypotheses.

With regard to body perception research more specifically, it is becoming clearer that category selectivity in ventral temporal cortex cannot be completely reduced to task-invariant processing of visual features (Peelen & Downing, 2017; Bi, Wang, & Caramazza, 2016; Harel, Kravitz, & Baker, 2014). Instead, category-selective responses reflect knowledge of what the object means to the observer, as well as how they interact with it (Peelen & Downing, 2017). As such, a wider neural architecture is likely to be important to consider. The reviewed studies begin to probe the boundary conditions that control the relationship between functional segregation and integration and identify which neural circuits interact with ventral temporal cortex and in which social contexts. But integration research is only beginning to scratch the surface of understanding this complex topic and much more research is needed.

A deeper appreciation of network science approaches to body perception may have clinical relevance for body-related disorders. For example, in anorexia nervosa, reduced connectivity between FBA and EBA has been associated with body image distortion (Suchan et al., 2013). More generally, therefore, when considering distortions in body image, it may prove useful to consider the role of wider networks. Problems in body-related information processing may arise from altered integration of body representations as much as altered responses in the ventral visual stream alone.

LIMITATIONS AND FUTURE DIRECTIONS

The current review had a purposely narrow focus and did not set out to provide a comprehensive review of body perception research from a cognitive neuroscience perspective. Instead, the review targeted human fMRI research that investigated body perception using measures of functional connectivity. As such, a comprehensive review of body perception research was beyond the scope of this review. Moreover, detailed reviews have already considered the proposed functions of EBA and FBA (Downing & Peelen, 2011), as well as the contribution from neurostimulation and patient studies to understanding body perception (Downing & Peelen, 2016), and the role of emotion in body perception (de Gelder et al., 2010; de Gelder, 2006). In addition, other work has used direct intracranial recordings in humans (Pourtois,

Peelen, Spinelli, Seeck, & Vuilleumier, 2007) and evidence from nonhuman primates (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2009; Pinsk et al., 2009; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005) to further understand the neural bases of body perception.

A further consideration also relates to the intended scope of the current review. The current article was centered on understanding functional connectivity within the ventral visual stream as well as between the ventral visual stream and broader neural networks. This focus was motivated by the dominance of the ventral visual stream in person perception research to date (Kanwisher, 2010). However, recent body perception research has also shown that coupling between extended networks makes a contribution to emotional body perception (Engelen, Zhan, Sack, & de Gelder, 2018; Poyo Solanas et al., 2018). For example, using fMRI, Poyo Solanas and colleagues (2018) showed that, when faces and bodies convey congruent compared with incongruent emotional signals, there is greater functional coupling between the amygdala and the ACC. This suggests that the amygdala may provide a regulatory role in responding to unambiguous emotional signals, which are conveyed by face and body concurrently. The results also suggest that coupling in body perception need not be restricted functional interactions that involve the ventral visual stream and future research should pursue this line of research further.

Further future directions stem from three principle limitations of the current evidence. First, a lack of emphasis on functional integration in body perception research hampers understanding of social perception more broadly. Except for models of emotional body perception, which include distributed networks (de Gelder, 2006), there is little research on body perception more generally that considers functional integration and network approaches. Building on the work reviewed here, further research is required that investigates the boundary conditions that demarcate the reliance on segregated processing in local modules and information processing that is distributed more widely across larger neural networks.

Second, evidence for functional integration in body perception is largely based on correlational data sets. Further methodological development will circumvent a reliance on correlational measures of functional connectivity and increase the prevalence of measures that permit inferences regarding directional (e.g., DCM, Granger causality), structural (e.g., diffusion tensor imaging), and causal relationships (e.g., using neurostimulation techniques combined with fMRI). Finally, functional connectivity studies should embrace best practice from open science (Munafò et al., 2017). For example, an increase in sample sizes will increase statistical power and may also permit analyses based on individual differences across the sample (Dubois & Adolphs, 2016). Moreover, using approaches from neuropsychology, as well as body dis-

orders, has shown promise in understanding mechanisms of body perception and should be used wherever possible.

Third, theories and models of body perception, which include functional integration, currently lack detail and precision. Updated theories of body perception should consider integration as much as segregation, as well as the extent to which particular processes are positioned along a segregation–integration continuum. By doing so, this would build a model of social perception, which stipulates a relative mix between segregation and integration. To aid the articulation of such theories, researchers may consider using theory mapping as a tool to develop, illustrate, and compare theories (Gray, 2017; www.theorymaps.org). Theory mapping provides a common language to visualize theories and store them online, thus promoting easier information exchange. The development of theories and models will enable more precise predictions to be made, thus providing a stronger test of the underlying hypothesis (Meehl, 1990). Harnessing the extensive development of network science approaches, which include graph theory, will also be vital for more sophisticated techniques for specifying and testing models of functional integration with brain data (Bullmore & Sporns, 2009).

Conclusion

Although bodies cue a range of inferences, which are instrumental for guiding social behavior, we currently know little about the neural organization of body perception. The current review of evidence from fMRI studies demonstrates that body perception is not restricted to processing in the ventral visual stream but instead reflects a functional alliance between the ventral visual stream and extended neural systems associated with action perception, executive functions, and theory of mind. Overall, these findings demonstrate how body percepts are constructed through interactions in distributed brain networks and underscore that functional segregation and integration should be considered together when formulating neurocognitive theories of body perception. By emphasizing the importance of network science approaches, the findings have implications for understanding network models of perception and cognition more generally, as well as understanding the biological bases of body image disturbances, such as anorexia nervosa, which are likely to have a complex biological basis.

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Note

1. The term “module” refers only to functionally related brain regions. It does not refer to additional features that were initially proposed by Jerry Fodor to define information processing modules (Fodor, 1983).

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