Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain.

Original
Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain / Borra, Elena; Luppino, Giuseppe. - In: CORTEX. - ISSN 0010-9452. - 118:(2019), pp. 19-37. [10.1016/j.cortex.2018.09.024]

Availability:
This version is available at: 11381/2856286 since: 2022-01-20T11:20:16Z

Publisher:
Masson SpA

Published
DOI:10.1016/j.cortex.2018.09.024

Elsevier Editorial System(tm) for CORTEX
Manuscript Draft

Manuscript Number: CORTEX-D-18-00433R1

Title: Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain

Article Type: SI:The Evolution of the Mind

Keywords: Comparative neuroscience; Evolution; Grasping; Oculomotor control; Gaze perception

Corresponding Author: Professor Giuseppe Luppino,

Corresponding Author's Institution: University of Parma

First Author: Elena Borra

Order of Authors: Elena Borra; Giuseppe Luppino

Abstract: The extent to which neural circuits and mechanisms underlying sensory, motor, and cognitive cortical functions in the human brain are shared with those of other animals, especially non-human primates, is currently a key issue in the field of comparative neuroscience. Cortical functions result from the conjoint function of different, reciprocally connected areas working together as large-scale functionally specialized networks, which can be investigated in human subjects thanks to the development of non-invasive functional and connectional imaging techniques. In spite of their limitations in terms of spatial and temporal resolution, these techniques make it possible to address the issue of how and to what extent the neural mechanisms for different cortical functions differ from those of non-human primates. Indeed, 30 million years of independent evolution have resulted in significant differences between the brains of humans and macaques, which are the experimental model system phylogenetically closest to humans for obtaining highly detailed anatomical and functional information on the organization of cortical networks. In the macaque brain, architectonic, connectional, and functional data have provided evidence for functionally specialized large-scale cortical networks involving temporal, parietal, and frontal areas. These networks appear to play a primary role in controlling different aspects of motor and cognitive motor functions, such as hand action organization and recognition, or oculomotor behavior and gaze processing. In the present review, based on the comparison of these data with data from human studies, we will argue that there is clear evidence for human counterparts of these networks. These human and macaque putatively homolog networks appear to share phylogenetically older neural mechanisms, which, in the evolution of the human lineage, could have been exploited and differentiated, resulting in the emergence of human-specific higher-order cognitive functions. These considerations are fully in line with the notion of "neural reuse" in primate evolution.

Cover Letter

UNIVERSITÀ
DI PARMA

DIPARTIMENTO DI MEDICINA
E CHIRURGIA

Dear Karl,
Dear Michel,

We are submitting to you a revised version of the manuscript CORTEX-D-18-00433 entitled “Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain” for publication in the forthcoming Cortex Special Issue dedicated to the evolution of the mind and the brain.

In revising the manuscript, all the comments and suggestions of the reviewers have been carefully taken into account. In the Responses to Reviewer section, we describe in details the way in which we have responded to the comments of the referees.

We hope that, after these revisions, the present study can be considered acceptable for publication.

Best wishes,

Giuseppe

Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain

Elena Borra and Giuseppe Luppino

Department of Medicine and Surgery, Neuroscience Unit, University of Parma, Parma, Italy

E mail addresses: elena.borra@unipr.it (E. Borra); luppino@unipr.it (G. Luppino)

Corresponding author: Prof. Giuseppe Luppino, Dipartimento di Medicina e Chirurgia, Unità di Neuroscienze, Università di Parma, Via Volturno 39, I-43100 Parma, Italy. Phone: +390521903879; Fax: +390521903900; E mail: luppino@unipr.it

We sincerely thank the Reviewers for taking their time in reviewing our manuscript and for their positive comments. Their comments and suggestions have been very helpful for improving and examining more in depth the coverage of the topic of the present review.
The following is the detailed description of the way in which the comments of the Reviewers have been addressed.

Reviewer #1:

Comment
P. 6 L.2 There is a typo: "outstanding" should be "understanding".
Response
Done

Comment
P. 6 last paragraph: The authors state that: "The aim is to see to what extent cortical networks and mechanisms identified in the macaque brain are shared with the human brain and to what extent some cognitive…". What exactly is meant by "mechanisms" here? Please elaborate, since it is not so clear at the current stage.
Response
We specified that by "mechanisms" we meant "neural mechanisms".

Comment
The authors elaborate on certain large-scale networks. To this end, they review connectional, functional and certain cytoarchitectonic data. However, the definition of the networks and what exact criteria makes them distinct is lacking, or rather, is mostly defined on subjective qualitative criteria. How can we quantify the distinctness of networks? What would be a way forward for a network taxonomy beyond subjective qualitative criteria? The authors have performed a quantitative study (Caminiti et al 2017) and some of the currently discussed networks indeed appear as separate clusters in the aforementioned study. However, some areas (46v, 12r) that are currently parts of both networks, appear only in one (the green) in Caminiti et al. 2017. Should these areas be part of one network, more and why? Please elaborate on these issues.
Response
In the Introduction (Page 1, second and third para.) we have addressed in more detail the issue of the definition and organization of functionally specialized cortical networks. Specifically, we have noted that, considering that any cortical area can take part to different functionally specialized networks with a variable anatomical and functional selectivity, the composition of a given network could vary, based on the sets of data and criteria used for its definition.
We are sorry for some possible ambiguities about the involvement of areas 46v and 12r in the two networks. Actually, in the manuscript it is reported that both these areas are connectionally not homogeneous: a caudal sector of both the areas is connected with oculomotor areas, whereas a middle sector is connected with grasping-related areas. In the revised manuscript, we tried to improve the description of these data (page 8, lines 2-5) and the distinction between different VLPF sectors is now shown also in the figures. In the cluster analysis of Caminiti et al. (2017), which was based on the overall cortical connectivity pattern of each individual area, the caudal parts of areas 46v and 12r (c46vc and c12r in Caminiti et al.) and the "middle" part of these areas (r46vc and i12r in Caminiti et al.) resulted to belong to different clusters (posterior vs. ventral orbital prefrontal cluster, respectively).

Comment
As mentioned, the link with the mental continuity theory is rather suggestive. Moreover, there are certain evidence for the existence of new areas in humans. Of course, as the authors point out, this

is not easy to establish. It would be of use to enhance the clarity and impact of the review to sketch out a bit more in detail the premises of the mental continuity theory and then more explicitly state why the current evidence presented in the review enhance it. The authors might also find relevant the Neural Reuse theory of Anderson (Anderson, 2010). I have not elaborated on how the two theories map to each other, but they have a very large overlap.

Response

We thank the Reviewer for suggesting to consider the Neural Reuse theory of Anderson. In the revised manuscript, this theory has been discussed in the context of mental continuity and development of human-specific mental functions (Pages 20 and 21). The experimental data presented in the manuscript are now discussed in the light of this theory in the concluding remarks.

Comment

The review closes a bit abruptly. Please add a concluding paragraph with the key points that the authors would like to convey to the reader.

Response

In revising the manuscript, we have reorganized the final part. There is now a concluding part in the manuscript focusing on the key points of the article, that is that some sensorimotor circuits for grasping or oculomotor control have been conserved in primate evolution and reused for generating human-specific functions.

Reviewer #2

Comment

Compares networks defined using different techniques

Although the authors mention that the homologues are also defined based on the similarities in functional connectivity across species, their review mostly relies on human neuroimaging studies to identify the functional homologues. There are studies that try to map similarities and differences between species explicitly using the same technique. A discussion of the same is warranted, especially since some of these studies examine the networks being considered in the review: Vincent et al., 2007 Nature for parietal-frontal networks; Babapoor-Farrokhran et al. 2013 J Neurophysiology for oculomotor system; Neubert et al., 2014 Neuron for premotor cortex.

Response

We think that functional connectivity can undoubtedly be very helpful for describing dynamic interactions between areas which, based on anatomical data, are known to be connected each other. In the manuscript, in several instances, this type of experimental data have been reviewed.

In the introduction we have mentioned that this approach has been proposed as a possible tool for mapping large-scale networks in the human brain (Page 3, end of first para.). However, we have also mentioned that there is clear evidence that functional connectivity is related to, but distinct from, anatomic connectivity and, thus, it does not appear capable of providing truthful pictures of cortical networks as properly defined (Page 3, end of second para.). Just for example, Babapoor-Farrokhran et al. reported functional connectivity of the medial FEF with several areas including parietooccipital areas V6 and V6A, superior parietal areas MIP and 5d and, even more surprising, with the primary somatosensory cortex and the dorsal part (leg representation?) of the primary motor cortex. All these connections have never been reported in connectional studies based on neural tracers and are quite difficult to explain from the functional point of view. Similar examples could be find in the study of Neubert et al, as well as in virtually all studies of this type. Note that our criticisms concern only the validity of this approach for defining networks of interconnected areas and connectionally distinct brain regions.

Comment

Temporal lobe - discussion necessary

There is evidence for a substantial expansion and reorganization of the temporal lobe in the human brain. Many of the areas responsible for processing eye gaze information are located in a different place in the temporal cortex and their homologues remain controversial (see work by Doris Tsao, Andrew Bell, and David Perrett). The volume of literature examining this deserves recognition and discussion in the review.

Response

In revising the manuscript, we have noted that because of the great expansion of the rostral temporal cortex it is quite difficult to infer possible homologies between human and macaque temporal areas based on topological criteria (Page 14). However, in our review, we have based our comparative observations on a large number of functional studies that have suggested homologies of some specific regions of the human temporo-occipital cortex with some specific macaque temporal areas (Page 14). The works of Tsao and colleagues and Bell and colleagues have been now cited.

Comment

Minor suggestions for figures

Although the focus is on the large-scale network, homologue areas across species can be highlighted with the same color for a quick reference.

Given that the list of areas is "non exhaustive", it will be useful to mention the same in the figure caption.

Response

The Figures have been modified according to the suggestions of the Reviewer.

Large-scale temporo-parieto-frontal networks for motor and cognitive motor functions in the primate brain

Elena Borra and Giuseppe Luppino

Department of Medicine and Surgery, Neuroscience Unit, University of Parma, Parma, Italy

E mail addresses: elena.borra@unipr.it (E. Borra); luppino@unipr.it (G. Luppino)

Corresponding author: Prof. Giuseppe Luppino, Dipartimento di Medicina e Chirurgia, Unità di Neuroscienze, Università di Parma, Via Volturno 39, I-43100 Parma, Italy. Phone: +390521903879; Fax: +390521903900; E mail: luppino@unipr.it

ABSTRACT

The extent to which neural circuits and mechanisms underlying sensory, motor, and cognitive cortical functions in the human brain are shared with those of other animals, especially non-human primates, is currently a key issue in the field of comparative neuroscience. Cortical functions result from the conjoint function of different, reciprocally connected areas working together as large-scale functionally specialized networks, which can be investigated in human subjects thanks to the development of non-invasive functional and connectional imaging techniques. In spite of their limitations in terms of spatial and temporal resolution, these techniques make it possible to address the issue of how and to what extent the neural mechanisms for different cortical functions differ from those of non-human primates. Indeed, 30 million years of independent evolution have resulted in significant differences between the brains of humans and macaques, which are the experimental model system phylogenetically closest to humans for obtaining highly detailed anatomical and functional information on the organization of cortical networks. In the macaque brain, architectonic, connectional, and functional data have provided evidence for functionally specialized large-scale cortical networks involving temporal, parietal, and frontal areas. These networks appear to play a primary role in controlling different aspects of motor and cognitive motor functions, such as hand action organization and recognition, or oculomotor behavior and gaze processing. In the present review, based on the comparison of these data with data from human studies, we will argue that there is clear evidence for human counterparts of these networks. These human and macaque putatively homolog networks appear to share phylogenetically older neural mechanisms, which, in the evolution of the human lineage, could have been exploited and differentiated, resulting in the emergence of human-specific higher-order cognitive functions. These considerations are fully in line with the notion of "neural reuse" in primate evolution.

Keywords:

Comparative neuroscience; Evolution; Grasping; Oculomotor control; Gaze perception

1. Introduction

One long-debated key issue of comparative neuroscience is to what extent neural circuits and mechanisms underlying sensory, motor, and cognitive cortical functions in the human brain are shared with those of other animals, especially non-human primates.

The general view of the organization of the neural substrate for a given brain function has largely evolved over the years. The most accepted current view is that cortical functions are not localized to specific regions as supported by localizationism, but result from the conjoint function of different, reciprocally connected areas working together as large-scale functionally specialized networks (see, for example, Bressler & Menon, 2010; Catani et al., 2012a).

There are different views on the organization of these networks and on the way in which they could operate (for reviews on this issue, see Anderson, 2010; Bergeron, 2007; Caminiti et al. 2017; Sporns, 2013). According to a modular view, functionally specialized networks are structurally and functionally distinct entities operating largely independently with one another. However, very often individual regions or even areas appear to be engaged in different functions. Furthermore, data from animal models indicate that the connectional structure of the cortex supports complex patterns of interareal interaction promoting widespread influences among cortical areas. Accordingly, any area could be responsible of specific information processing operations that could be used for different functions, taking part in different functionally specialized large-scale networks.

Thus, the identification of these networks requires multidisciplinary integration of structural and functional data in order to extract from the general pattern of cortical connectivity those connections that could mediate dynamic interactions between different areas contributing to a specific function. In this context, it is noteworthy that, as the degree of anatomical and functional selectivity varies across areas, the composition of a given network could vary based on the sets of data and criteria used for its definition.

Based on this conceptual framework it becomes clear that understanding the neural circuits and mechanisms underlying specific cortical functions requires multimodal experimental approaches aiming to define the following: i) the exact localization and extent of the areas possibly involved in a specialized network; ii) the existence of connections among these areas, and iii) their possible specific functional contribution. All together, these data can provide comprehensive pictures of large-scale functionally specialized cortical networks in terms of nodes and edges (Sporns, 2013), possible flows of information processing, and neural mechanisms from which a given function can emerge.

In recent years, the development of non-invasive functional and connectional imaging techniques has made it possible to address the definition of large-scale, functionally specialized networks in the human brain. Indeed, functionally distinct cortical sectors can be identified using functional magnetic resonance imaging (fMRI), and brain connectivity can be investigated using diffusion-weighted MRI (dMRI). Furthermore, functional connectivity MRI has recently been proposed as a possible tool for mapping large-scale networks in the human brain.

However, a detailed definition of cortical networks in the human brain is still prevented by several limitations of these techniques. First, fMRI is limited in spatio-temporal resolution and gives indirect information of neuronal activity only at the macroscale level. Further, though multimodal techniques allow detailed post-mortem architectonic studies of the human cortex (see, Amunts & Zilles, 2015), the areal attribution of functional data obtained in living subjects can be, at best, based on probabilistic architectonic maps, which, to some extent, prevents univocal anatomo-functional correlations of experimental data. Second, recent studies in which well-known cortical pathways have been traced in macaques with dMRI have seriously questioned the technique's validity for precise in vivo tracing of point-to-point connectivity (Reveley et al., 2015; Thomas et al., 2014). Third, several observations have been made that functional connectivity is related to, but distinct from, anatomic connectivity, as it could be subserved by polysynaptic, as well as monosynaptic, anatomical circuits, and can be modulated by the task performed by the subjects or several other factors differently from structural connectivity (Biswal et al., 2010; Buckner et al., 2013). Thus, at present, this technique does not appear capable of providing truthful comprehensive pictures of large scale functionally specialized networks as properly defined.

In spite of these limitations, the exploitation of these techniques has made it possible to make comparative observations, thus addressing the issue of how and to what extent the neural mechanisms for different cortical functions differ across different primate species. These observations are essential for assessing the extent to which detailed functional and connectional data from non-human primate studies can be used for explaining the neural mechanisms of the human brain. Indeed, 30 million years of independent evolution have resulted in significant differences between the brains of humans and macaques, which are the experimental model system phylogenetically closest to humans for obtaining highly detailed anatomical and functional information (see, e.g., Passingham, 2009; Sereno & Tootell, 2005).

Humans have brains much larger than would be expected for primates of a similar body size, and this difference appears to reflect primarily an enlargement of the neocortex and, specifically, a disproportionate enlargement of the higher-order association cortex of the frontal, temporal, and parietal lobes, relative to the primary sensory and motor areas (see, e.g., Preuss, 2011). This selective expansion is considered the neural basis for the outstanding cognitive capabilities of humans (see, e.g., Chaplin et al., 2013; Passingham, 2009; Rilling et al., 2012; Sereno & Tootell, 2005).

However, it appears that the association cortex expanded in a predictable manner in primate evolution (see Preuss, 2011). Indeed, the human brain is not exceptional in its cellular composition, as it contains as many neurons as would be expected for a primate brain of human size (Herculano-Houzel, 2009), and the human frontal cortex is not larger than expected for a primate brain of human size (Semendeferi et al., 2002). Comparative observations also showed that the expansion of the cortex in simian primates of different brain size correlates with a disproportionate expansion of some association areas typically involved in complex cognitive and behavioral functions (Chaplin et al., 2013). Furthermore, Hill et al. (2010), by comparing human and macaque cerebral cortices, found that the pattern of human evolutionary expansion is remarkably similar to the pattern of human postnatal expansion, suggesting that those association areas which disproportionately expanded in primate evolution are those that mature later in human postnatal development. Finally, recent comparative observations showed a relationship between structural interindividual variability and evolutionary expansion in the primate brain in which regions that show a higher degree of variability in a series of MRI measures of grey and white matter are those that could have evolved more recently (Croxson et al., 2017). Accordingly, our understanding of cognitive capabilities could be simply due to the fact that our brain has a lot more association cortex in absolute terms than do other non-human primates (Preuss, 2011).

In line with these comparative evolutionary observations, a large body of experimental evidence has been provided supporting the notion that the monkey and human brain share common plans of anatomical and functional organization of sensory, motor, and cognitive functions likely inherited from the last common ancestor shared by modern humans and macaques (Caminiti et al., 2015; Geyer et al., 2000; Mantini et al., 2013; Orban et al., 2004).

In recent years, based on anatomical and functional data, we have provided evidence for functionally specialized large-scale cortical networks of the macaque brain involved in controlling different aspects of motor and cognitive motor functions. In the present review article, these data will be used to make comparative considerations, based on anatomical and functional data obtained in human studies. The aim is to see to what extent cortical networks and neural mechanisms identified in the macaque brain are shared with the human brain and to what extent some cognitive motor human-specific abilities could be the result of the exploitation and differentiation of neural mechanisms of the macaque brain.

2. A large-scale cortical network for controlling purposeful hand actions and for action recognition in the macaque

Fig. 1 shows the architecture of a large-scale temporo-parieto-frontal network of the macaque brain providing a possible substrate for interfacing perceptual, cognitive, and hand-related sensorimotor processes for controlling hand actions based on object identity, goals, and memory-based or contextual information. This network has been designated as *lateral grasping network* (Borra et al., 2017b).

The network is centered on a parieto-frontal circuit linking the two hand-related visuomotor areas F5 and AIP, located in the ventral premotor cortex (PMv) and in the inferior parietal lobule (IPL), respectively. This circuit plays a crucial role in mediating visuomotor transformations for grasping, in which visual coding of the object's physical properties (e.g., size, shape, orientation) automatically leads to the activation of potential motor acts appropriate for hand-object interactions (Jeannerod et al., 1995; Rizzolatti & Luppino, 2001). This process, also referred to as "affordances extraction" (see, e.g., Fagg & Arbib, 1998), primarily relies on visual coding of the object's physical properties, carried out along the occipito-parietal visual information processing pathway designated as the "dorsal visual stream" (Sakata et al., 1997). However, area AIP is also robustly connected to sectors of the inferotemporal cortex (Borra et al., 2008), located at the highest hierarchical levels of the occipito-temporal visual information processing pathway designated as the "ventral visual stream" and involved in object discrimination and recognition (see, e.g., Tanaka, 1996). One of these sectors, located in area TEa/m of the lower bank of the superior temporal sulcus, is part of a component of the ventral visual stream specifically dedicated to three-dimensional (3D) object and action processing (Orban et al., 2014). These temporal connections of area AIP provide the substrate for extraction of object affordances, carried out by the AIP–F5 circuit, based on information related not only to the intrinsic properties, but also to the identity of the object target of the action. Furthermore, they could provide the access of signals related to motor and haptic representations of hand actions to the representations of object identity, thus playing a role in the neural mechanisms underlying tactile object recognition.

Area F5 is robustly connected with two other parietal areas, the visuomotor hand-related area PFG of the IPL convexity and the hand field of the higher order somatosensory area SII of the parietal operculum. In area PFG, grasping-related activity appears to be influenced by the context in which the action is performed, possibly reflecting sequential action organization according to its goal or motor intention (Bonini et al., 2010, 2011, 2012; Fogassi et al., 2005). Furthermore, the finding that area PFG grasping neurons can integrate information on both grip type and action goal suggests that this IPL area encodes information about both “how” and “why” each motor act has to be done (Bonini et al., 2012). In area SII, the presence of neurons in the hand field preferentially responsive to proprioceptive input and often responding well to active movements, especially when grasping objects, suggests this area plays a role in the somatomotor transformations for object-oriented hand actions and in haptic processing of object shapes (Fitzgerald et al., 2004).

The PMv area F5 and the two IPL areas AIP and PFG also host another class of visuomotor hand-related neurons—designated as “mirror neurons”— which activate during the execution of hand motor acts, as well as during the observation of similar acts done by others (Gallese et al., 1996; Rizzolatti et al., 1996). This neural activity has been interpreted as the result of visuomotor transformations in which observed actions are mapped on their corresponding internal motor representations. It has been suggested that these neurons are part of an observation-execution matching system (mirror system) which is the basis for the ability to recognize others’ goal-directed motor acts (see Rizzolatti et al., 2014). There is evidence that visual information on observed actions can be provided to the PMv-IPL components of the mirror system through the temporal connectivity of areas AIP and PFG. Specifically, fMRI data obtained in awake macaques (Nelissen et al., 2011) showed that action observation activates cortical sectors located in both the ventral and the dorsal banks of the STS. One sector, located in the ventral bank, corresponds to the TEa/m sector connected to area AIP. Another sector, located in the upper bank of the STS, corresponds to a sector of the superior temporal polysensory (STP) area connected to the PFG. Area STP is a higher-order multisensory area which integrates information within and across modalities (Baylis et al., 1987; Bruce et al., 1981) and hosts visual neurons (see Carey et al., 1997), coding biological motion, differentiating between self-produced actions and actions made by others, and coding the intentionality of actions (Jellema et al., 2000; Jellema & Perrett, 2003), suggesting a role in social cognition. Based on these data, Nelissen et al. (2011) suggested that visual action information, encoded in the STS, is forwarded to parietal areas of the mirror system along a TEa/m-AIP pathway which could provide visual descriptions of the type and immediate goal of hand actions made by others, and along a STP-PFG pathway which could be involved in extracting the intention behind the observed motor act. It is also noteworthy that the SII region hosts visually responsive neurons, active during the observation of human actions or objects, suggesting that this area has a role in multisensory integration for motor control and in action recognition (Hihara et al., 2015).

All these parietal areas and the anterior sector of area F5 (F5a) are also differentially connected with specific sectors of the areas 46v and 12r, located in the ventrolateral prefrontal cortex (VLPF). The prefrontal cortex is a large, heterogeneous region considered, as a whole, to be critically involved in the so-called “executive functions”, a term that, in general, refers to those mechanisms by which behavioral performance is optimized in situations requiring cognitive processes (see Tanji & Hoshi, 2008). Recent data provided evidence of rostrocaudal connectional gradients in the VLPF, in which the caudal part is primarily connected with inferior parietal and prearcuate oculomotor areas, the middle part with parietal and frontal sensorimotor areas, and the rostral part primarily with other prefrontal areas (Borra et al., 2011; Gerbella et al., 2010, 2013). Functional studies have indeed shown that cells active in tasks requiring oculomotor responses (e.g., Averbeck et al., 2006; Boch & Goldberg, 1989; Ichihara-Takeda & Funahashi, 2007) and the execution of arm/hand responses (Bruni et al., 2015; Hoshi et al., 1998, 2000; Requin et al., 1990; Simone et al., 2015) tend to be located more caudally and more rostrally in the caudal VLPF, respectively. In the context of the *lateral grasping network*, area 46v could be involved in selecting, monitoring, and updating object-oriented hand actions based on behavioral goals and guiding rules and current, memorized, or working memory information on motor programs. Furthermore, area 12r, which is robustly connected with the same sector of area TEa/m which is connected to area AIP (Borra et al., 2011), is a possible substrate for integration of the ventral visual stream with sensorimotor hand-related information in the prefrontal cortex. Thus, in the intermediate part of area 12r, the retrieval, retention, and manipulation of information on objects or hand-object interactions could be finalized to the control of object-oriented hand actions and to tactile object recognition. The finding that, in this VLPF hand-related sector, there are neurons which respond to the observation of goal-directed actions also suggests this sector's participation in the action observation-execution matching system (Simone et al., 2017).

Finally, all the various parietal, premotor, and VLPF hand-related areas are connected with a specific sector located relatively dorsally in the dysgranular insula (see Borra et al., 2017b). This sector appears to overlap, at least in part, with an insular zone from which intracortical microstimulation evokes hand movements (Jezzini et al., 2012). This specific insular sector is a possible source of signals related to internal states (Ibañez et al., 2010) modulating the control of hand actions.

Based on these data, a model has been proposed in which motor programs of "potential" hand motor acts are first activated in area F5 as a consequence of fast visuomotor transformations, and then selected based on behavioral goals, contextual information, and memorized information on object identity and properties (Borra et al., 2017b). The selected hand motor acts can then be put into action through the robust connections of the posterior sector of F5 (F5p), from which intracortical microstimulation evokes hand movements at relatively low current thresholds, with the hand field of the primary motor area F1 (Borra et al., 2010). There is evidence that the projections from F5p to F1 could provide the substrate for generating the various muscle synergies (movements) represented in F1 which are necessary for executing the motor act selected at the level of F5 (Cerri et al., 2003; Prabhu et al., 2009; Shimazu et al., 2004; Umilta et al., 2007). However, F5p is also a source of projections to the brainstem and the spinal cord, suggesting a contribution by this area to the generation and control of hand movements in parallel with the hand field of F1 (Borra et al., 2010).

The lateral grasping network, as shown in Fig. 1, is not exhaustive. First, there is connectional evidence for the participation in this network of other components, such as the granular frontal opercular area GrFO. Second, there are areas which, based on their premotor connectivity, appear to contribute almost equally well to more than one network, suggesting a more general role in motor control. One of these areas is the medial premotor area F6 (pre-SMA), involved in higher-order aspects of motor control (see, e.g., Picard & Strick, 2001; Nachev et al., 2008), which could play a role in forwarding signals which transform potential actions into actual movements and determine movement onset, and in controlling the temporal organization of motor programs (see Ridderinkhof et al., 2011; Rizzolatti et al., 2014). This area also hosts neurons selectively encoding others' actions and neurons showing activity increase associated with another's errors, suggesting involvement in action recognition (Yoshida et al., 2011, 2012).

3. Cortical networks for explorative and communicative oculomotor behavior in the macaque

In addition to the lateral grasping network, there is evidence for another large-scale temporo-parieto-frontal network, in which the various nodes are linked through "dorsal" temporo-parieto-frontal and "ventral" temporo-frontal pathways, which could play a crucial role in controlling some aspects of oculomotor behavior.

As shown in Fig. 2, this network is centered on a parieto-frontal circuit linking two visually responsive oculomotor areas: the lateral intraparietal (LIP) area located in the lateral bank of the intraparietal sulcus just caudal to area AIP and the frontal eye field (FEF) located in the anterior bank of the arcuate sulcus. This circuit plays a crucial role in visuomotor transformations for controlling saccadic eye movements and in the orientation of spatial attention (see Lynch & Tian, 2006; Wardak et al., 2011). The FEF, defined as the arcuate bank sector from which intracortical microstimulation evokes saccades at relatively low current thresholds, displays a topographic organization in which smaller and larger amplitude saccades are evoked from more ventral and more dorsal sites, respectively (Bruce et al., 1985). The FEF is also connected with the supplementary eye field (SEF), located rostrally in the dorsal premotor cortex, and with several caudal prefrontal areas, including areas 8r, 45B, and 45A, and the caudal sectors of areas 12r, 46v, and 46d (Gerbella et al., 2010; Huerta et al., 1987; Schall et al., 1995; Stanton et al., 1993, 1995). All these caudal prefrontal areas/sectors are, in turn, connected to the SEF and, except for caudal 12r and 45A, to area LIP (Borra et al. 2011, 2017b; Gerbella et al., 2010, 2013). Thus, all these areas appear involved in the oculomotor frontal system. Furthermore, the FEF and the various caudal prefrontal oculomotor areas are provided with an access to brainstem oculomotor centers (Borra et al., 2015).

As for the parieto-frontal circuitry involved in controlling hand actions, the visuomotor transformations for controlling oculomotor behavior also appear to rely not only on input from dorsal visual stream areas, but also on input from both the lower and the upper banks of the STS, which appear to differentially distribute in the parieto-frontal oculomotor circuitry. Specifically, area LIP, the ventral part of the FEF, areas 45B and caudal 12r are connected to several inferotemporal sectors of the lower bank of the STS and of the inferotemporal convexity cortex (Blatt et al., 1990; Cavada & Goldman-Rakic, 1989; Gerbella et al., 2010; Schall et al., 1995; Stanton et al., 1995). One of these sectors, located in the ventral bank of the STS, is just caudal to the sector involved in the lateral grasping network. This sector is part of the ventral visual stream component specifically dedicated to 3D object and action processing (Denys et al., 2004; Nelissen et al., 2011) and also activates during the execution of visually guided eye movements (Ward et al., 2015). Accordingly, it is possible to define a large-scale temporo-parieto-frontal network involving area LIP, ventral FEF, area 45B, and caudal TEa/m, where visuospatial dorsal visual stream information and ventral visual stream information on objects and actions could be used for guiding small-amplitude saccades.

Indeed, area LIP, the ventral part of the FEF, and area 45B host neurons showing shape selectivity, encoding non-spatial attributes of the stimuli, and activating during the observation of two-dimensional (2D) shapes, thus likely reflecting input from ventral visual stream areas (Peng et al., 2008; Sereno & Maunsell, 1998; Toth & Assad, 2002). Furthermore, fMRI data have revealed area 45B activation for the observation of objects, faces, and actions (Denys et al., 2004; Nelissen et al., 2005; Tsao et al., 2008b). Though the functional properties of area 45B still remain to be fully elucidated, fMRI (Premereur et al., 2015) and 2-deoxyglucose (Moschovakis et al., 2004) data have shown activation during the execution of saccades, fitting well with the proposed affiliation of this area with the oculomotor frontal system, as indicated by its connectivity pattern. It has proposed that area 45B is a “pre-oculomotor” area involved in guiding the exploration of visual scenes for the perception of objects, actions, and faces (Gerbella et al., 2010). Other caudal prefrontal oculomotor areas connected to LIP and the ventral part of the FEF (8r, caudal 46v), as well as caudal 12r, could play a role in executive functions aimed at the control of small saccades and could contribute to the suggested role of area LIP in representing salience maps combining visual information with cognitive factors, such as behavioral context, task difficulty, or reward information (Wardak et al., 2010).

Connectional data provide evidence for a further partially overlapping large-scale oculomotor network involving area STP and the fundal STS area IPa, which are connected to area LIP, the dorsal part of the FEF, the SEF, and area 45A (Blatt et al., 1990; Cavada & Goldman-Rakic, 1989; Gerbella et al., 2010; Huerta & Kaas, 1990; Luppino et al., 2001; Saleem et al., 2014; Stanton et al., 1995). As mentioned above, area STP is involved in processing various forms of biological motion, including the direction of gaze and head, which may be relevant in understanding where the conspecifics are fixating (Carey et al., 1997; Jellema et al., 2000; Mistlin & Perrett, 1990) and is involved in the integration of audiovisual communication signals (Barraclough et al., 2005; Chandrasekaran & Ghazanfar, 2008; Dahl et al., 2009). Reversible inactivation of the posterior STP severely disrupts gaze-following behavior (Roy et al., 2014). Furthermore, in area LIP, there are neurons which become more active both while directing attention toward a region of space and while observing other monkeys doing the same (Shepherd et al., 2009). These “mirror” oculomotor responses likely reflect input from the STS and suggest that area LIP plays a role in sharing attention with others (Shepherd, 2010). Area 45A is a caudal VLPF area involved in the multisensory processing of communication stimuli (Diehl & Romanski, 2014; Romanski & Averbeck, 2009; Sugihara et al., 2006), and it activates during action and face observation (Nelissen et al., 2005; Tsao et al., 2008b; Kuraoka et al., 2015), suggesting it has a role in communication behavior. Moreover, this area is robustly connected to the dorsal part of the FEF, is a source of projections to subcortical oculomotor structures (Borra et al., 2015), and is activated during the execution of eye movements (Premereur et al., 2015).

Thus, there is connectional evidence for a large-scale oculomotor network involving areas STP-IPa, LIP, 45A, and dorsal FEF, which could provide the substrate for the role of gaze position and eye movement in social behavior, thus contributing to an understanding of the social intentions of other individuals (Ghazanfar et al., 2006; Shepherd, 2010). Moreover, the rostral part of area 46d, which is connected to area STP, dorsal FEF and area 45A (Borra et al., 2017a), could play a higher-order executive role in this “social oculomotor” network. In this context, it is noteworthy that other oculomotor areas, such as the SEF, appear to be involved in both these described networks and that nodes of these two networks, together with other areas, could participate in large-scale networks involved in other aspects of oculomotor behavior.

4. Possible human counterpart of the macaque lateral grasping/action recognition network

In early functional imaging studies and in others since then (Binkofski et al., 1998; Culham et al., 2003; Ehrsson et al., 2000; Johnson-Frey, 2004; Toni et al., 2001), it has been shown that the execution of object-oriented hand actions activates two cortical zones located in the frontal lobe and in the IPL, respectively. The frontal zone is located mostly in the ventral part of the precentral gyrus and also extends rostrally into the inferior frontal gyrus (IFG), involving Brodmann's architectonic area 44 (Brodmann, 1909), corresponding to the caudal part of the language-related Broca's region. The IPL zone corresponds to both the rostral part of the lateral bank of the IPS and the supramarginal gyrus (SMG). Based on their location, these two zones have been considered as the possible human counterparts of the macaque PMv and IPL areas of the *lateral grasping network*, respectively. Several studies have provided further evidence for these proposed homologies. Specifically, Fornia et al. (2018) showed that short-train or single-pulse electrical stimulation of the cortical surface along the dorso-ventral extent of the PMv is effective in evoking hand, orofacial, and combined orofacial and hand motor responses from the dorsal, ventral, and intermediate part of it, respectively, providing evidence for a somatotopic arrangement of this region similar to that of the macaque F5. Furthermore, transcranial magnetic stimulation (TMS) studies showed an interaction of the dorsal part of the PMv with the primary motor cortex, modulated during grasping execution, and that a virtual lesion of this PMv sector impairs grasping execution (Davare et al., 2006, 2008, 2009). These data provide support for the possible homology between this human PMv sector and the posterior subdivision of the macaque area F5 (F5p). Other studies showed that the lateral bank of the IPS also activates during surface orientation discrimination and subsequent related spatial adjustment of finger position (Shikata et al., 2003) and is involved in 3D shape processing from disparity (Georgieva et al., 2009) and in coding intrinsic object properties (Monaco et al., 2015). Furthermore, this region hosts neurons selectively tuned for motor imagery of specific hand shapes (Klaes et al., 2015) and TMS studies have shown that virtual lesions of this zone affect hand shaping, scaling of grip force (Dafotakis et al., 2008; Davare et al., 2007), and online adjustments of goal-directed hand actions (Rice et al., 2006; Tunik et al., 2005). Finally, there is an increase in effective connectivity between this region and PMv when grasping small objects (Grol et al., 2007) and a reduction in PMv–M1 interactions during grasping preparation after a virtual lesion of this hand-related zone of the IPS (Davare et al., 2010). These data have provided strong support for the possible homology between this anterior intraparietal hand-related sector (human area AIP) and the macaque area AIP.

Execution of object-oriented actions (Gazzola & Keysers, 2009; Grèzes & Decety, 2001) also activates the SMG, which appears to be involved in comparing predicted and actual sensory input during object manipulation and updating of sensorimotor memories (Jenmalm et al., 2006). Furthermore, TMS of this region (but also of the caudal IFG) affects planning of sequential goal-directed hand actions in which object grasping is embedded in actions with different goals (Tunik et al., 2008). The human rostral IPL hosts a cluster of architectonic areas which, based on dMRI observations, appears to share several connectional features with the macaque rostral IPL areas (Caspers et al., 2006, 2011, 2013; Ruschel et al., 2014). One of these areas, area PFt, has been considered the putative homolog of the macaque area PFG (Caspers et al., 2011).

Finally, there is evidence that the human parietal operculum hosts two architectonically distinct somatosensory areas, designated as OP1 and OP4 (Eickhoff et al., 2006a,b, 2007). Data from dMRI studies suggested connectivity of these two areas with rostral IPL and PMv areas and with Broca’s region (Eickhoff et al., 2010). Functional imaging data showed that this region activates during both tactile stimulation (Burton et al., 2008; Disbrow et al., 2000; Eickhoff et al., 2007) and movement execution (Gazzola & Keysers, 2009; Hinkley et al., 2007) and is involved in tactile object recognition (Reed et al., 2004). Furthermore, TMS studies provided evidence for a causal role of this region in the haptic working memory of object properties and grasping motor programs (Cattaneo et al., 2015; Maule et al., 2015). These data provided clear support for the proposed homology between this human opercular region (human SII) and the macaque SII region (Eickhoff et al., 2006a,b, 2007).

Though technical limitations still prevent reliable dMRI definition of point-to-point anatomical connectivity in the human brain, several studies have provided evidence for anatomical connectivity between the rostral IPL and the PMv/IFG (Hecht et al., 2013; Ramayya et al., 2010; Rushworth et al., 2006; Schubotz et al., 2010), which, as in macaques, is largely supported by the third branch of the superior longitudinal fasciculus (SLF; Schmahmann et al., 2007; Thiebaut de Schotten et al., 2012). In sum, in the human brain, there is a possible parieto-frontal circuitry linking the PMv/IFG with the rostral IPL and parietal operculum, which very likely represents the human counterpart of the macaque parieto-frontal circuitry at the core of the lateral grasping network. These possible homologies appear even more plausible considering that the PMv/IFG, the human area AIP, the SMG (especially area PFt), and the human SII all activate during the observation of goal-directed hand actions, thus also suggesting involvement of this possible parieto-frontal circuitry in action recognition (human mirror system), as in macaques (Caspers et al., 2010; Fogassi & Simone, 2013; Gazzola & Keysers, 2009; Rizzolatti et al., 2014).

In recent years, evidence has been accumulated indicating that, as in macaques, human visuomotor processing for selecting and controlling hand actions carried out in area AIP is influenced by processing which takes place in the ventral visual stream areas (see van Polanen & Davare, 2015).

Comparisons between the human and the macaque temporal cortex based on merely topological criteria are complicated by the great expansion of language-related and other higher-order associative areas in the evolution of the human lineage. Comparative fMRI observations have provided clear evidence for human homologs of the macaque visual extrastriate and adjacent temporal areas, which, however, appear to be located more posteriorly and medially than their macaque counterparts (for reviews on this issue, see Orban et al., 2004, 2014). Specifically, there is evidence for a cortical sector located ventral to the human homolog of the motion sensitive area MT, in the posterior inferior temporal and the fusiform gyrus (the lateral occipital complex, or LOC) in which different sites are specifically active during the visual processing of shapes, faces, and actions (e.g., Bell et al., 2009; Denys et al., 2004; Jastorff & Orban, 2009; Kanwisher et al., 1997; Malach et al., 1995;Tsao et al., 2008a). Based on comparative fMRI observations, Denys et al. (2004) proposed that the LOC could be the human homolog of the lower bank of the STS (area TEa/m) and the laterally adjacent IT convexity cortex in macaques.

Indeed, grasping objects based on the processing of pictorial depth cues increases the activity of the human area AIP and its functional connectivity with the PMv and the lateral occipital complex (LOC) (Verhagen et al., 2008). Furthermore, when planning object-oriented actions, there are activity patterns in the LOC reflecting the type of hand action (Gallivan et al., 2013a), and the organization of visual object representations in this region reflects action-related properties of the objects (Bracci et al., 2012; Bracci & Peelen, 2013; Mahon et al., 2007; Peelen et al., 2013). Finally, the visual and haptic coding of objects activates the human area AIP (Grefkes et al., 2002) and a part of the LOC (Amedi et al., 2002; James et al., 2002; Reed et al., 2004), providing evidence for the multimodal representation of objects in the human ventral visual stream and suggesting an interaction between area AIP and the LOC for tactile object recognition (Lacey et al., 2009; Tal & Amedi, 2009).

In the human temporal cortex, rostral to MT and dorsal to the LOC, there is a region including the posterior STS (pSTS) and middle temporal gyrus (MTG) involved in multisensory processing and responsive to diverse types of biological motion (Allison et al., 2000; Frith & Frith, 2007), which appears to be the putative homolog of the macaque area STP (Beauchamp et al., 2008). Biological motion processing in this region appears to mostly concern kinematic aspects, whereas, in the LOC, it appears to mostly concern configuration changes of the observed actions, suggesting, as in macaques, a dual-stream processing of action observations (Jastorff & Orban, 2009). These sectors of the pSTS/MTG and LOC are considered the major source of visual action information for the human mirror system (Caspers et al., 2010; Grosbras et al., 2012; Molenberghs et al., 2012; Rizzolatti et al., 2014).

In the human brain, there is a conspicuous fiber system linking the human rostral IPL with the posterior part of the superior, middle, and inferior temporal gyri, which has been identified as the posterior segment of the arcuate or of the SLF (Catani et al., 2005; Martino et al., 2013; Wu et al., 2016). Connectivity between the STG and SMG could also be supported by the middle longitudinal fasciculus (Makris et al., 2016). Thus, it is possible that human temporo-parietal connectivity includes components equivalent to the macaque pathways connecting TEa/m with area AIP and area STP with area PFG, and that the human temporal cortex includes areas which take part in what is possibly the human counterpart of the macaque lateral grasping/action recognition network.

To our knowledge, there is no clear evidence for activation of prefrontal areas other than the IFG during the mere execution or the observation of hand-object interactions. However, there is clear clinical, electrophysiological, and imaging evidence for the involvement of the human middle frontal gyrus (MFG)—for the most part, the putative homolog of the macaque ventral area 46 (Petrides, 2005)—in different aspects of the executive control of motor behavior (Goldenberg & Spatt, 2009; Haaland et al., 2000; Rowe et al., 2005) including hand actions. Indeed, TMS over this region affects free selection of hand actions (Hadland et al., 2001) and modulates the excitability of the primary motor cortex, showing temporally and spatially selective interaction between these two areas (Hasan et al., 2013). Furthermore, functional imaging evidence showed involvement of the MFG during the preparation of contralateral and ipsilateral hand actions (Gallivan et al., 2013b). Finally, the MFG displays visual object-related activation (Denys et al., 2004), activates during texture recognition (Stylianou-Korsnes et al., 2010), and also appears to be involved in tactile object recognition (Lacey et al., 2010; Reed et al., 2004; Savini et al., 2010). Cieslik et al. (2013) have suggested a rostrocaudal subdivision of the MFG into two distinct subregions in which the caudal one is characterized by functional connectivity with bilateral intraparietal sulci, including the location of the human area AIP and appears to be more strongly related to action execution and working memory. The second and the third branches of the SLF connecting the IPL with the frontal lobe (Makris et al., 2005; Thiebaut de Schotten et al., 2012) and the frontal inferior longitudinal tract connecting the precentral gyrus with the MFG (Catani et al., 2012b; Rojkova et al., 2016) could represent the possible substrate for the participation of this region in the putative human counterpart of the lateral grasping/action recognition network. Furthermore, the inferior fronto-occipital fasciculus, linking temporal areas (including the LOC and caudal temporal areas) with prefrontal areas (including the MFG) (Sarubbo et al., 2013; Thiebaut de Schotten et al., 2012) could provide the substrate for a connectivity equivalent to the macaque inferotemporal connectivity with hand-related VLPF areas. However, note that in the human brain there is a component of the arcuate fasciculus (long direct segment, Catani et al., 2005), directly connecting the temporal with the frontal cortex, for which there is no equivalent in the macaque brain (Rilling et al., 2008).

Functional data have also provided evidence for a putative human homolog of the hand-related sector of the macaque insula, which activates during the execution and observation of hand actions with a vitality form, suggesting a modulation of the cortical circuits for controlling hand actions according to the internal state of the individual (Di Cesare et al., 2014, 2015). Observations based on dMRI have provided evidence for the connectivity of the insula with the PMv, the IFG, the MFG, and the IPL (Cerliani et al., 2012; Di Cesare et al., 2018; Ghaziri et al., 2015).

Finally, the rostral part of the medial premotor cortex, based on architectonic and functional data, has been considered the homolog of the macaque area F6/pre-SMA (Geyer et al., 2000; Nachev et al., 2008; Picard & Strick, 1996; Zilles et al., 1996). As in the macaque, this area appears to play a more general role in several higher-order aspects of motor control (see Geyer et al., 2012; Nachev et al., 2008). Specifically, recent evidence showed that the human pre-SMA could play a role, together with the IFG, in the neural mechanisms underlying response inhibition (Angelini et al., 2015; Aron et al., 2007; Swann et al., 2012). A bundle of fibers connecting the pre-SMA and the rostral SMA with the PMv/IFG, designated as the frontal aslant tract (Catani et al., 2012b; Rojkova et al., 2016), is likely the substrate for this interaction.

In sum, there is robust evidence that, in the human brain, there is a set of potentially linked parietal, temporal, and frontal areas, which, as a result of their topology and functional properties, appear very likely to form a human counterpart of the macaque lateral grasping/action observation network.

However, this same set of cortical nodes, or at least part of it, also appears to be involved in cognitive abilities unique or almost unique to humans, such as higher-order aspects of organization of object-oriented actions, including tool use (Johnson-Frey et al., 2005; Peeters et al., 2009, 2013; Ramayya et al., 2010), imitation, and imitation learning (Buccino et al., 2004). Specifically, functional studies have shown that tool use action planning, execution, and observation and tool observation and naming activate a set of cortical regions of the left hemisphere, including the LOC and posterior MTG in the temporal cortex, the anterior IPS and SMG in the parietal cortex, and the PMv/IFG and MFG in the frontal cortex, which largely overlap with the putative human lateral grasping/action observation network (Brandi et al., 2014; Choi et al., 2001; Johnson-Frey et al., 2005; Moll et al., 2000; Peeters et al., 2009, 2013). Based on comparative observations in humans and macaques, Peeters et al. (2009, 2013) have concluded that the left rostral SMG also includes an evolutionarily new human-specific zone specifically devoted to tool use, which could have differentiated from phylogenetically older rostral IPL hand-related areas.

Furthermore, there is evidence that imitation or imitation learning of hand actions activates temporal, rostral IPL, and PMv/IFG regions involved in action observation and, especially for imitation learning, the MFG (Buccino et al., 2004; Caspers et al., 2010; Higuchi et al., 2012; Rizzolatti et al., 2014; Vogt et al., 2007). Based on comparative dMRI observations, Hecht et al. (2013) have suggested that stronger and more extensive connectivity of the SMG with the pSTS/MTG and LOC regions involved in shape and action coding, as well as stronger connectivity between the SMG and PMv/IFG, differentiate the cortical mirror system of humans from that of macaques and could have contributed to the emergence of the role of this system in imitation and imitation learning (see also Rizzolatti et al., 2014). Furthermore, the differentiation of the MTG areas responsible for storing conceptual and semantic information about tools and of the rostral SMG sector devoted to tool use, and their interconnectivity, could have contributed to the emergence of tool use from a specialization of neural mechanisms for controlling hand-object interactions shared with macaques (Orban & Caruana, 2014; Peeters et al., 2009, 2013; Ramayya et al., 2010).

5. Possible human counterpart of the macaque networks for explorative and communicative oculomotor behavior

A large number of human functional studies have shown that tasks requiring the execution of visually- or memory-guided saccades and/or shifts of attention in the visual field activate several foci located in the posterior parietal and frontal cortex (e.g., Alvarez et al., 2010; Corbetta et al., 1998; Curtis & Connolly, 2008; Dieterich et al., 2009; Petit et al., 1997; Petit & Haxby, 1999; Koyama et al., 2004). In the posterior parietal cortex, one of these foci, observed in virtually all studies, is located dorsally and posteriorly in the medial bank of the IPS in a sector which has been designated as the dorsal IPS medial (DIPSM, see Orban et al., 2004) and is usually referred to as the “parietal eye field” (PEF). Based on different lines of functional evidence, there is a general consensus that this sector corresponds to the macaque area LIP (Orban, 2016). The finding that the possible human equivalent of the macaque area LIP is located in the medial, and not in the lateral bank of the IPS, is an example of the possible differences in the topology of equivalent areas between the macaque and human brains, which, in this case, could be accounted for by the disproportionate increase of the human IPL. Some studies (e.g., Corbetta et al., 1998; Koyama et al., 2004) have also described additional foci, one of them located more rostrally in the IPS, whose possible macaque equivalent still remains to be verified. In the frontal cortex, one focus constantly observed in all studies is located within the dorsal part of the precentral sulcus at the junction with the superior frontal sulcus. There is unanimous consensus that this sector corresponds to the macaque FEF. However, the exact location of this field tends to vary across different studies. According to a high-resolution fMRI study, this field is located in the anterior bank of the precentral sulcus and corresponds to a distinct chemoarchitectonic area (Rosano et al., 2002, 2003). An additional, constantly observed focus is located in the medial frontal gyrus and is considered to correspond to the macaque SEF. Furthermore, several studies have provided evidence for at least one additional frontal oculomotor field located ventral to the human FEF in the precentral sulcus and usually referred to as the "inferior" FEF (Amiez & Petrides, 2009; Corbetta et al., 1998; Derrfuss et al., 2012; Heide et al., 2001; Koyama et al., 2004; Luna et al., 1998; Mort et al., 2003). Though varying in location across studies, this field has been usually attributed to Brodmann area 6 (Brodmann, 1909) and an homology with a possible oculomotor premotor field of the macaque brain has been then suggested (Amiez & Petrides, 2009; Koyama et al., 2004). However, evidence for a postarcuate oculomotor field in the macaque brain is not univocally supported by fMRI data (Baker et al., 2006; Koyama et al., 2004; Premereur et al., 2015), nor is it supported by electrophysiological studies. Furthermore, the attribution of this field to Brodmann area 6, does not necessarily imply that it is actually a premotor field located within architectonic area 6. Indeed, the human FEF is also located within the limits of Brodmann area 6 but, as reviewed above, is a distinct architectonic granular area (Rosano et al., 2003) and a homolog of a macaque prefrontal area (area 8/FEF). It is noteworthy that all the above mentioned studies have not considered that, in the macaque caudal prefrontal cortex, there are several oculomotor areas, including area 45B, which are located just ventral to the FEF and, as reviewed in Section 3, activate during the execution of saccadic eye movements. Finally, Patel et al. (2015) found that, in human subjects, visuospatial attentional tasks activated, in addition to the FEF, two other fields, one apparently located ventral to the inferior FEF in the precentral sulcus and the other located in the inferior frontal sulcus. Additional comparative observations are needed in order to examine the possible homologies between the human and the macaque frontal oculomotor systems in the light of data showing a multiplicity of caudal oculomotor prefrontal areas in the macaque.

All together, these data provide evidence for a parieto-frontal circuit corresponding to the macaque LIP-FEF circuit involved in oculomotor control and in a dorsal attention network for controlling spatial and featural attention (Corbetta & Shulman, 2002). The SLFI could provide the substrate for the connectivity in the human brain between the PEF and the FEF, as suggested by Thiebaut de Shotten et al. (2011) and, possibly, between the PEF and other frontal oculomotor fields. In fact, dMRI evidence for connectivity between the SPL and inferior frontal areas has been provided by Hecht et al. (2013).

Functional studies have also suggested the interaction of ventral visual stream areas with the parieto-frontal oculomotor circuitry. For example, Preston et al. (2013) have shown that, in a visual search task, the LOC appears to play a role in coding the contextual location of objects and features in real scenes, and they suggested that information on the likely location of the targets could be relayed from the LOC to the parieto-frontal oculomotor network for directing attention to the contextually relevant location.

Furthermore, there is evidence that parietal and frontal oculomotor areas are also involved in the neural mechanisms underlying gaze perception and joint attention, together with temporal areas (Bristow et al., 2007; Grosbras et al., 2005; Hooker et al., 2003; Nummenmaa & Calder, 2009; Williams et al., 2005; see also Shepherd, 2010). Specifically, the involved temporal regions include the posterior STS/MTG specialized for perceiving social signals mediated by biological motion including gaze shifts (Allison et al., 2000; Blakemore et al., 2004; Caruana et al., 2014; Marquardt et al., 2017) and the fusiform/LOC regions specialized for face processing, which can be modulated by the configuration of the gaze (George et al., 2001). In the frontal lobe, in addition to the FEF, some studies have observed activation in a more ventral region involving the IFG (Hooker et al., 2003) or the junction between the inferior frontal sulcus and the precentral sulcus (inferior frontal junction, IFJ, Bristow et al., 2007; Grosbras et al., 2005; Nummenmaa & Calder, 2009). It is noteworthy that a cortical zone located at the IFJ was found to activate during the observation of faces only when the eyes were not masked (Chan & Downing, 2011). These data suggest homology of this region with the macaque area 45A.

In the human brain, there is evidence, based on dMRI and fiber dissection observations, for a temporal connectivity of the SPL. Specifically, these connections appear to involve, in the temporal cortex, the rostral and caudal regions located in the STG, MTG, and ITG, including the fusiform gyrus and, in the SPL, the caudal part corresponding to Brodmann's area 7 (Hecht et al., 2013; Kamali et al., 2014; Makris et al., 2009, 2013, 2016; Wang et al., 2013; Wu et al., 2016). These connections appear to run through the MdLF and a component of the AF/SLF (Makris et al., 2009, 2013, 2016; Kamali et al., 2014; Wang et al., 2013; Wu et al., 2016). This temporo-SPL fiber system has been described as evolutionarily new, not present in the macaque brain (e.g., Hecht et al., 2013; Wang et al., 2013), and as a possible substrate for a role of the human SPL in action observation (Abdollahi et al., 2013) or visuo-auditory attentional processing (Hecht et al., 2013; Makris et al., 2016; Wang et al., 2013). However, it is possible that components of this connectivity are equivalent to the temporal connectivity of the macaque area LIP. Furthermore, it is possible that components of the arcuate fasciculus and inferior fronto-occipital fasciculus linking temporal to frontal areas are equivalent to the temporal connections of the macaque frontal oculomotor areas.

All together, these data suggest that, as in the macaque, the human brain hosts a large-scale temporo-parieto-frontal circuitry for oculomotor control, covert shift of attention, and gaze perception. Accordingly, humans and non-human primates appear to share neural circuits and mechanisms for basic gaze-following behavior, which, in humans, could have been the foundation for more sophisticated social skills, such as mutual awareness of shared mental states (Shepherd, 2010).

6. Human-specific functions vs. human-specific areas

It is largely agreed in comparative neuroscience that primates share common principles of cortical organization. Indeed, primates display similar layouts of homologous sensory, motor, and association areas organized in similar sensorimotor domains, which, to a large extent, can be identified even in prosimians (Kaas & Stepniewska, 2016). Furthermore, there are very strong similarities in the organization of the major fiber tracts connecting parietal with frontal areas (Schmahmann et al., 2007; Thiebaut de Schotten et al., 2012). Accordingly, primates appear to share common plans of the organization of sensorimotor functions, which have been likely conserved along the various lineages that have differentiated during primate evolution.

In the evolution of the lineage leading to *Homo sapiens*, there have also been substantial changes in brain size and organization, which are considered to be at the basis of some higher-order human- or almost human-specific cognitive functions. According to Darwin’s theory, the evolution of complex structures is incremental, so that human specific mental functions would derive from phylogenetically older mental processes with gradual evolutionary trajectories. However, it has been proposed that human-specific mental functions reflect discontinuities pervading nearly every domain of cognition (Penn et al., 2008). De Waal and Ferrari (2010) have argued that the concept of discontinuity results from the adoption of a “top-down” perspective in comparative cognitive research in which the main question is which animals possess or do not possess a given cognitive ability. Conversely, if a “bottom-up” approach is adopted, focusing on the constituent capacities underlying larger cognitive phenomena, it appears quite clear that the basic building blocks of cognition might be shared across a wide range of species, suggesting mental continuity in primate evolution (Sherwood et al., 2008; de Waal & Ferrari, 2010). In line with this view, there are theories positing that one central organizational principle of the functional structure of the brain is based on reuse of neural, often sensorimotor, circuitries for various cognitive purposes (“neural reuse theories”, see Anderson, 2010). Specifically, according to these theories “neural circuits established for one purpose are commonly exapted (exploited, recycled, redeployed) during evolution or normal development, and put to different uses, often without losing their original functions” (Anderson, 2010). Two of these theories differ on the time course over which they operate. One – the massive redeployment theory (Anderson, 2007) – concerns the evolutionary emergence of the functional organization of the brain, the other – the neuronal recycling theory (Dehaene, 2005; Dehaene and Cohen, 2009)– explains those cognitive abilities for which there has been insufficient time for specialized neural circuits to have evolved.

Taken for granted that in primate evolution neural reuse for developing progressively more complex cognitive abilities has been paralleled by a disproportionate increase in size of some cortical regions, one important issue is to what extent regional expansions have resulted in the generation of evolutionary new cortical areas.

In addressing this issue, it is important first to note what makes a cortical area. It is largely accepted that the cerebral cortex contains many distinct entities, usually referred to as ‘‘areas,’’ although it has been matter of debate what precisely constitutes a cortical area and what the best criteria for their definition are (see, e.g., Van Essen, 1985). In general, three main criteria, the architectonic, the connectional, and the functional, are considered most useful for the definition of a cortical area. Converging evidence, based on these criteria, is generally considered a strong argument for reliable identification and delineation of a cortical area (see, e.g., Felleman & Van Essen, 1991; Van Essen, 1985). For example, in macaques, the IPL convexity cortex has been subdivided into four distinct areas based on converging architectonic (Gregoriou et al., 2006), connectional (Rozzi et al., 2006), and functional (Rozzi et al., 2008) evidence.

In human studies, the term “area” is very often simply used to designate cortical zones which appear to have specific functional properties. However, the functional distinctiveness of a given cortical zone does not necessarily imply that it corresponds to a distinct area as defined above. Indeed, a functionally distinct cortical zone could correspond to a module of a larger cortical area, or could extend over adjacent cortical areas which share some common functional features. Unfortunately, the issue of the areal attribution of functional data, even when addressed, is often seriously prevented by the coarseness of the architectonic maps for several brain regions. It is noteworthy, however, that, for some human cortical regions, a higher functional complexity seems not to be paralleled by a higher architectonic complexity, with respect to the corresponding regions of the macaque brain. This appears to be the case of the parietal lobe in which detailed architectonic studies have identified a number of superior parietal, intraparietal, and inferior parietal areas almost comparable to those of the macaque (Caspers et al., 2006; Choi et al., 2006; Scheperjans et al., 2008). For example, in the inferior parietal lobule, the evolutionarily new human-specific tool use SMG zone appears to be located within architectonic area PFt, which also activates during hand action execution, observation, and imitation and has been considered the possible homolog of the macaque area PFG (Caspers et al., 2010, 2011; Gazzola & Keysers, 2009; Peeters et al., 2009). Conversely, in some human cortical regions, the architectonic organization appears to be more complex than in the corresponding regions of the macaque brain. This is the case, for example, of the caudal IFG, which, based on chemoarchitectonic data, has been subdivided into several areas (Amunts et al., 2010) that could in part correspond to evolutionarily new areas not present in the macaque brain. In sum, there is no compelling evidence that evolutionarily new cognitive capacities in humans are necessarily linked to the addition of evolutionarily new cortical areas as properly defined (e.g., Preuss, 2011; Sherwood et al., 2008).

7. Concluding remarks

In the present article we have reviewed comparative observations showing that some human- or almost human-specific functions, such as tool use, imitation learning, and language, appear to involve cortical zones of the parietal and frontal cortex which overlap or, at least, are in contiguity with the nodes of the human counterpart of the macaque lateral grasping/action recognition network. These observations suggest that neural mechanisms underlying tool use could have emerged from the exploitation and adaptation of phylogenetically older neural mechanisms, shared with macaques, underlying the selection and control of object-oriented hand actions (see, e.g., Orban & Caruana, 2014). Similarly, imitation and imitation learning could have emerged from the exploitation and adaptation of phylogenetically older neural mechanisms, shared with macaques, involved in mapping observed actions into their corresponding motor representations (see e.g., Rizzolatti et al., 2014). It has been also suggested that the neural mechanism for recognizing actions made by others (mirror mechanism) could have represented a neural prerequisite for the development of interindividual communication and, finally, of speech (Rizzolatti & Arbib, 1998; Pulvermüller, 2018). Similar considerations could be done also for the neural mechanisms underlying some higher-order aspects of social attention and interactions based on gaze perception, which appear to involve cortical nodes of the putative human counterpart of the macaque networks for explorative and communicative oculomotor behavior (Nummenmaa & Calder, 2009; Shepherd, 2010).

In sum, data reviewed above provide clear examples of the fact that the monkey and the human brain share neural circuits for sensory, motor, and cognitive motor functions, likely inherited from the last common ancestor and the neural mechanisms mediated by these circuits could have represented building blocks for the generation, based on a process of neural reuse, of higher order human specific functions. Obviously, the degree of detail of this type of comparative observations would greatly benefit from a desirable future development of non-invasive techniques for a more detailed definition of point-to-point cortical connectivity and the structural correlation of functional data.

Acknowledgements

The work from our laboratory has been supported by Ministero dell’Istruzione, dell’Università e della Ricerca (grant number: PRIN 2015, 2015AWSW2Y_005) and by the European Commission Grant Cogsystems FP7-250013.

References

Abdollahi RO, Jastorff J, Orban GA. 2013. Common and segregated processing of observed actions in human SPL. Cereb Cortex. 23:2734–2753.

Allison T, Puce A, McCarthy G. 2000. Social perception from visual cues: role of the STS region. Trends Cogn Sci. 4:267–278.

Alvarez TL, Alkan Y, Gohel S, Douglas Ward B, Biswal BB. 2010. Functional anatomy of predictive vergence and saccade eye movements in humans: a functional MRI investigation. Vision Res. 50:2163–2175.

Amedi A, Jacobson G, Hendler T, Malach R, Zohary E. 2002. Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb cortex. 12:1202–1212.

Amiez C, Petrides M. 2009. Anatomical organization of the eye fields in the human and non-human primate frontal cortex. Prog Neurobiol. 89:220–230.

Amunts K, Lenzen M, Friederici AD, Schleicher A, Morosan P, Palomero-Gallagher N, Zilles K. 2010. Broca's region: novel organizational principles and multiple receptor mapping. PLoS Biol.8. pii: e1000489. doi: 10.1371/journal.pbio.1000489.

Amunts K, Zilles K. 2015. Architectonic mapping of the human brain beyond Brodmann. Neuron. 88:1086–1107.

Anderson ML. 2007. The massive redeployment hypothesis and the functional topography of the brain. Philosophical Psychology 21:143–74.

Anderson ML. 2010. Neural reuse: a fundamental organizational principle of the brain. Behav Brain Sci. 33:245–66. doi: 10.1017/S0140525X10000853

Angelini M, Calbi M, Ferrari A, Sbriscia-Fioretti B, Franca M, Gallese V, Umiltà MA. 2015. Motor Inhibition during overt and covert actions: an electrical neuroimaging study. PLoS One. 10:e0126800.

Aron AR, Behrens TE, Smith S, Frank MJ, Poldrack RA. 2007. Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. J Neurosci. 27:3743–3752.

Averbeck BB, Sohn J-W, Lee D. 2006. Activity in prefrontal cortex during dynamic selection of action sequences. Nat Neurosci. 9:276–282.

Baker JT, Patel GH, Corbetta M, Snyder LH. 2006. Distribution of activity across the monkey cerebral cortical surface, thalamus and midbrain during rapid, visually guided saccades. Cereb Cortex. 16:447–459.

Barraclough NE, Xiao DK, Baker CI, Oram MW, Perrett DI. 2005. Integration of visual and auditory information by superior temporal sulcus neurons responsive to the sight of actions. J

Cogn Neurosci. 17:377–391.

Baylis GC, Rolls ET, Leonard CM. 1987. Functional subdivisions of the temporal lobe neocortex. J Neurosci. 7:330–342.

Beauchamp MS, Yasar NE, Frye RE, Ro T. 2008. Touch, sound and vision in human superior temporal sulcus. Neuroimage. 41:1011–1020.

Bell AH, Hadj-Bouziane F, Frihauf JB, Tootell RB, Ungerleider LG. 2009. Object representations in the temporal cortex of monkeys and humans as revealed by functional magnetic resonance imaging. J Neurophysiol. 101:688-700. doi: 10.1152/jn.90657.2008.

Bergeron V. 2007. Anatomical and functional modularity in cognitive science: shifting the focus. Philosophical Psychology 20:175–195.

Binkofski F, Dohle C, Posse S, Stephan KM, Hefter H, Seitz RJ, Freund HJ. 1998. Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. Neurology. 50:1253–1259.

Biswal BB, Mennes M, Zuo X-N, Gohel S, Kelly C, Smith SM, Beckmann CF, Adelstein JS, Buckner RL, Colcombe S, Dogonowski A-M, Ernst M, Fair D, Hampson M, Hoptman MJ, Hyde JS, Kiviniemi VJ, Kötter R, Li S-J, Lin C-P, Lowe MJ, Mackay C, Madden DJ, Madsen KH, Margulies DS, Mayberg HS, McMahon K, Monk CS, Mostofsky SH, Nagel BJ, Pekar JJ, Peltier SJ, Petersen SE, Riedl V, Rombouts SARB, Rypma B, Schlaggar BL, Schmidt S, Seidler RD, Siegle GJ, Sorg C, Teng G-J, Veijola J, Villringer A, Walter M, Wang L, Weng X-C, Whitfield-Gabrieli S, Williamson P, Windischberger C, Zang Y-F, Zhang H-Y, Castellanos FX, Milham MP. 2010. Toward discovery science of human brain function. Proc Natl Acad Sci U S A. 107:4734–4739.

Blakemore S-J, Winston J, Frith U. 2004. Social cognitive neuroscience: where are we heading? Trends Cogn Sci. 8:216–222.

Blatt GJ, Andersen RA, Stoner GR. 1990. Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. J Comp Neurol. 299:421–445.

Boch RA, Goldberg ME. 1989. Participation of prefrontal neurons in the preparation of visually guided eye movements in the rhesus monkey. J Neurophysiol. 61:1064–1084.

Bonini L, Rozzi S, Serventi FU, Simone L, Ferrari PF, Fogassi L. 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. Cereb Cortex. 20:1372–1385.

Bonini L, Ugolotti Serventi F, Simone L, Rozzi S, Ferrari PF, Fogassi L. 2011. Grasping neurons of monkey parietal and premotor cortices encode action goals at distinct levels of abstraction during complex action sequences. J Neurosci. 31:5876–5886.

Bonini L, Ugolotti Serventi F, Bruni S, Maranesi M, Bimbi M, Simone L, Rozzi S, Ferrari PF, Fogassi L. 2012. Selectivity for grip type and action goal in macaque inferior parietal and ventral premotor grasping neurons. J Neurophysiol. 108:1607–1619.

Borra E, Belmalih A, Calzavara R, Gerbella M, Murata A, Rozzi S, Luppino G. 2008. Cortical connections of the macaque anterior intraparietal (AIP) area. Cereb Cortex. 18:1094–1111.

Borra E, Belmalih A, Gerbella M, Rozzi S, Luppino G. 2010. Projections of the hand field of the macaque ventral premotor area F5 to the brainstem and spinal cord. J Comp Neurol. 518:2570–2591.

Borra E, Ferroni CG, Gerbella M, Giorgetti V, Mangiaracina C, Rozzi S, Luppino G. 2017a. Rostro-caudal connectional heterogeneity of the dorsal part of the macaque prefrontal area 46. Cereb Cortex. 1–20.

Borra E, Gerbella M, Rozzi S, Luppino G. 2011. Anatomical evidence for the involvement of the macaque ventrolateral prefrontal area 12r in controlling goal-directed actions. J Neurosci. 31:12351–12363.

Borra E, Gerbella M, Rozzi S, Luppino G. 2015. Projections from caudal ventrolateral prefrontal areas to brainstem preoculomotor structures and to basal ganglia and cerebellar oculomotor loops in the macaque. Cereb Cortex. 25:748–64.

Borra E, Gerbella M, Rozzi S, Luppino G. 2017b. The macaque lateral grasping network: a neural substrate for generating purposeful hand actions. Neurosci Biobehav Rev. 75:65–90.

Bracci S, Cavina-Pratesi C, Ietswaart M, Caramazza A, Peelen M V. 2012. Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. J Neurophysiol. 107:1443–1456.

Bracci S, Peelen M V. 2013. Body and object effectors: the organization of object representations in high-level visual cortex reflects body-object interactions. J Neurosci. 33:18247–18258.

Brandi ML, Wohlschlager A., Sorg C, Hermsdorfer J. 2014. The neural correlates of planning and executing actual tool use. J Neurosci. 34:13183–13194.

Bressler SL, Menon V. 2010. Large-scale brain networks in cognition: emerging methods and principles. Trends Cogn Sci. 14:277–290.

Bristow D, Rees G, Frith CD. 2007. Social interaction modifies neural response to gaze shifts. Soc Cogn Affect Neurosci. 2:52–61.

Brodmann K. 1909. Vergleichende Lokalisationslehre der Gro hirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Leipzig: Johann Ambrosius Barth.

Bruce CJ, Desimone R, Gross CG. 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. J Neurophysiol. 46:369–384.

Bruce CJ, Goldberg ME, Bushnell MC, Stanton GB. 1985. Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements. J Neurophysiol. 54:714–734.

Bruni S, Giorgetti V, Bonini L, Fogassi L. 2015. Processing and integration of contextual information in monkey ventrolateral prefrontal neurons during selection and execution of goal-directed manipulative actions. J Neurosci. 35:11877–11890.

Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G. 2004. Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. Neuron. 42:323–334.

Buckner RL, Krienen FM, Yeo BTT. 2013. Opportunities and limitations of intrinsic functional connectivity MRI. Nat Neurosci. 16:832–837.

Burton H, Sinclair RJ, Wingert JR, Dierker DL. 2008. Multiple parietal operculum subdivisions in humans: tactile activation maps. Somatosens Mot Res. 25:149–162.

Caminiti R, Innocenti GM, Battaglia-Mayer A. 2015. Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans. Neurosci Biobehav Rev. 56:73–96.

Caminiti R, Borra E, Visco-Comandini F, Battaglia-Mayer A, Averbeck BB, Luppino G. 2017. Computational architecture of the parieto-frontal network underlying cognitive-motor control in monkeys. eNeuro. 4. pii: ENEURO.0306-16.2017. doi: 10.1523/ENEURO.0306-16.2017.

Carey DP, Perrett DI, Oram MW. 1997. Recognizing, understanding and reproducing action. In: Boller F, Grafman J, editors. Handbook of Neuropsychology, volII. Amsterdam: Elsevier. p. 111–130.

Caruana F, Cantalupo G, Russo G Lo, Mai R, Sartori I, Avanzini P. 2014. Human cortical activity evoked by gaze shift observation: An intracranial EEG study. Hum Brain Mapp. 35:1515–1528.

Caspers S, Eickhoff SB, Rick T, von Kapri A, Kuhlen T, Huang R, Shah NJ, Zilles K. 2011. Probabilistic fibre tract analysis of cytoarchitectonically defined human inferior parietal lobule areas reveals similarities to macaques. Neuroimage. 58:362–380.

Caspers S, Geyer S, Schleicher A, Mohlberg H, Amunts K, Zilles K. 2006. The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. Neuroimage. 33:430–448.

Caspers S, Schleicher A, Bacha-Trams M, Palomero-Gallagher N, Amunts K, Zilles K. 2013. Organization of the human inferior parietal lobule based on receptor architectonics. Cereb Cortex. 23:615–628.

Caspers S, Zilles K, Laird AR, Eickhoff SB. 2010. ALE meta-analysis of action observation and imitation in the human brain. Neuroimage. 50:1148–1167.

Catani M, Dell'Acqua F, Bizzi A, Forkel SJ, Williams SC, Simmons A, Murphy DG, Thiebaut de Schotten M. 2012a. Beyond cortical localization in clinico-anatomical correlation. Cortex. 48:1262–1287.

Catani M, Dell'Acqua F, Vergani F, Malik F, Hodge H, Roy P, Valabregue R, Thiebaut de Schotten M. 2012b. Short frontal lobe connections of the human brain. Cortex. 48:273–291.

Catani M, Jones DK, ffytche DH. 2005. Perisylvian language networks of the human brain. Ann Neurol. 57:8–16.

Cattaneo L, Maule F, Tabarelli D, Brochier T, Barchiesi G. 2015. Online repetitive transcranial magnetic stimulation (TMS) to the parietal operculum disrupts haptic memory for grasping. Hum Brain Mapp. 0:n/a-n/a.

Cavada C, Goldman-Rakic PS. 1989. Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. J Comp Neurol. 287:422–445.

Cerliani L, Thomas RM, Jbabdi S, Siero JCW, Nanetti L, Crippa A, Gazzola V, D'Arceuil H, Keysers C. 2012. Probabilistic tractography recovers a rostrocaudal trajectory of connectivity variability in the human insular cortex. Hum Brain Mapp. 33:2005–2034.

Cerri G, Shimazu H, Maier MA, Lemon RN. 2003. Facilitation from ventral premotor cortex of primary motor cortex outputs to macaque hand muscles. J Neurophysiol. 90:832–842.

Chan AW-Y, Downing PE. 2011. Faces and eyes in human lateral prefrontal cortex. Front Hum Neurosci. 5:51.

Chandrasekaran C, Ghazanfar AA. 2008. Different neural frequency bands integrate faces and voices differently in the superior temporal sulcus. J Neurophysiol. 101:773–788.

Chaplin TA, Yu H-H, Soares JGM, Gattass R, Rosa MGP. 2013. A conserved pattern of differential expansion of cortical areas in simian primates. J Neurosci. 33:15120–15125.

Choi HJ, Zilles K, Mohlberg H, Schleicher A, Fink GR, Armstrong E, Amunts K. 2006. Cytoarchitectonic identification and probabilistic mapping of two distinct areas within the anterior ventral bank of the human intraparietal sulcus. J Comp Neurol. 495:53–69.

Choi SH, Na DL, Kang E, Lee KM, Lee SW, Na DG. 2001. Functional magnetic resonance imaging during pantomiming tool-use gestures. Exp brain Res. 139:311–317.

Cieslik EC, Zilles K, Caspers S, Roski C, Kellermann TS, Jakobs O, Langner R, Laird AR, Fox PT, Eickhoff SB. 2013. Is there "one" DLPFC in cognitive action control? Evidence for heterogeneity from co-activation-based parcellation. Cereb Cortex. 23:2677–2689.

Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL. 1998. A common network of functional areas for attention and eye movements. Neuron. 21:761–773.

Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci. 3:201–215.

Croxson PL, Forkel SJ, Cerliani L, Thiebaut de Schotten M. 2017. Structural variability across the primate brain: a cross-species comparison. Cereb Cortex. 1–13.

Culham JC, Danckert SL, DeSouza JFX, Gati JS, Menon RS, Goodale MA. 2003. Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. Exp brain Res. 153:180–189.

Curtis CE, Connolly JD. 2008. Saccade preparation signals in the human frontal and parietal cortices. J Neurophysiol. 99:133–145.

Dafotakis M, Sparing R, Eickhoff SB, Fink GR, Nowak DA. 2008. On the role of the ventral premotor cortex and anterior intraparietal area for predictive and reactive scaling of grip force. Brain Res. 1228:73–80.

Dahl CD, Logothetis NK, Kayser C. 2009. Spatial organization of multisensory responses in temporal association cortex. J Neurosci. 29:11924–11932.

Davare M, Andres M, Clerget E, Thonnard JL, Olivier E. 2007. Temporal dissociation between hand shaping and grip force scaling in the anterior intraparietal area. J Neurosci. 27:3974–3980.

Davare M, Andres M, Cosnard G, Thonnard JL, Olivier E. 2006. Dissociating the role of ventral and dorsal premotor cortex in precision grasping. J Neurosci. 26:2260–2268.

Davare M, Lemon R, Olivier E. 2008. Selective modulation of interactions between ventral premotor cortex and primary motor cortex during precision grasping in humans. J Physiol. 586:2735–2742.

Davare M, Montague K, Olivier E, Rothwell JC, Lemon RN. 2009. Ventral premotor to primary motor cortical interactions during object-driven grasp in humans. Cortex. 45:1050–1057.

Davare M, Rothwell JC, Lemon RN. 2010. Causal connectivity between the human anterior intraparietal area and premotor cortex during grasp, Current Biology. 20:176–81. doi: 10.1016/j.cub.2009.11.063.

de Waal FBM, Ferrari PF. 2010. Towards a bottom-up perspective on animal and human cognition. Trends Cogn Sci. 14:201–207.

Dehaene S. 2005. Evolution of human cortical circuits for reading and arithmetic: The “neuronal recycling” hypothesis. In: From monkey brain to human brain, ed. S. Dehaene, J.-R. Duhamel, M. D. Hauser & G. Rizzolatti, pp. 133–57. MIT Press.

Dehaene S, & Cohen L. 2007. Cultural recycling of cortical maps. Neuron 56:384–98.

Denys K, Vanduffel W, Fize D, Nelissen K, Peuskens H, Van Essen D, Orban GA. 2004. The processing of visual shape in the cerebral cortex of human and nonhuman primates: a functional magnetic resonance imaging study. J Neurosci. 24:2551–65.

Derrfuss J, Vogt VL, Fiebach CJ, von Cramon DY, Tittgemeyer M. 2012. Functional organization of the left inferior precentral sulcus: dissociating the inferior frontal eye field and the inferior frontal junction. Neuroimage. 59:3829–3837.

Di Cesare G, Di Dio C, Marchi M, Rizzolatti G. 2015. Expressing our internal states and understanding those of others. Proc Natl Acad Sci U S A. 112:10331–10335.

Di Cesare G, Di Dio C, Rochat MJ, Sinigaglia C, Bruschweiler-Stern N, Stern DN, Rizzolatti G. 2014. The neural correlates of “vitality form” recognition: an fMRI study: this work is dedicated to Daniel Stern, whose immeasurable contribution to science has inspired our research. Soc Cogn Affect Neurosci. 9:951–960.

Di Cesare G, Pinardi C, Carapelli C, Caruana F, Marchi M, Gerbella M, Rizzolatti G. 2018. Insula connections with the parieto-frontal circuit for generating arm actions in humans and macaque monkeys. Cereb Cortex. 2018 May 7. doi: 10.1093/cercor/bhy095.

Diehl MM, Romanski LM. 2014. Responses of prefrontal multisensory neurons to mismatching faces and vocalizations. 34:11233–11243.

Dieterich M, Müller-Schunk S, Stephan T, Bense S, Seelos K, Yousry TA. 2009. Functional magnetic resonance imaging activations of cortical eye fields during saccades, smooth pursuit, and optokinetic nystagmus. Ann N Y Acad Sci. 1164:282–292.

Disbrow E, Roberts T, Krubitzer L. 2000. Somatotopic organization of cortical fields in the lateral sulcus of Homo sapiens: evidence for SII and PV. J Comp Neurol. 418:1–21.

Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H. 2000. Cortical activity in precision- versus power-grip tasks: an fMRI study. J Neurophysiol. 83:528–536.

Eickhoff SB, Amunts K, Mohlberg H, Zilles K. 2006a. The human parietal operculum. II. Stereotaxic maps and correlation with functional imaging results. Cereb Cortex. 16:268–279.

Eickhoff SB, Grefkes C, Zilles K, Fink GR. 2007. The somatotopic organization of cytoarchitectonic areas on the human parietal operculum. Cereb Cortex. 17:1800–1811.

Eickhoff SB, Jbabdi S, Caspers S, Laird AR, Fox PT, Zilles K, Behrens TEJ. 2010. Anatomical and functional connectivity of cytoarchitectonic areas within the human parietal operculum. J

Neurosci. 30:6409–6421.

Eickhoff SB, Schleicher A, Zilles K, Amunts K. 2006b. The human parietal operculum. I. Cytoarchitectonic mapping of subdivisions. Cereb Cortex. 16:254–267.

Fagg AH, Arbib M a. 1998. Modeling parietal-premotor interactions in primate control of grasping. Neural Networks. 11:1277–1303.

Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex. 1:1–47.

Fitzgerald PJ, Lane JW, Thakur PH, Hsiao SS. 2004. Receptive field properties of the macaque second somatosensory cortex: evidence for multiple functional representations. J Neurosci. 24:11193–11204.

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. 2005. Parietal lobe: from action organization to intention understanding. Science. 308:662–667.

Fogassi L, Simone L. 2013. The mirror system in monkeys and humans and its possible motor-based functions. Adv Exp Med Biol. 782:87–110.

Fornia L, Ferpozzi V, Montagna M, Rossi M, Riva M, Pessina F, Martinelli Boneschi F, Borroni P, Lemon RN, Bello L, Cerri G. 2018. Functional characterization of the left ventrolateral premotor cortex in humans: a direct electrophysiological approach. Cereb Cortex. 28:167–183.

Frith CD, Frith U. 2007. Social cognition in humans. Curr Biol. 17:R724–R732.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G. 1996. Action recognition in the premotor cortex. Brain. 119:593–609.

Gallivan JP, Chapman CS, McLean DA, Flanagan JR, Culham JC. 2013a. Activity patterns in the category-selective occipitotemporal cortex predict upcoming motor actions. Eur J Neurosci. 38:2408–2424.

Gallivan JP, McLean DA., Flanagan JR, Culham JC. 2013b. Where one hand meets the other: limb-specific and action-dependent movement plans decoded from preparatory signals in single human frontoparietal brain areas. J Neurosci. 33:1991–2008.

Gazzola V, Keysers C. 2009. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. Cereb Cortex. 19:1239–1255.

George N, Driver J, Dolan RJ. 2001. Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. Neuroimage. 13:1102–1112.

Georgieva S, Peeters R, Kolster H, Todd JT, Orban GA. 2009. The processing of three-dimensional shape from disparity in the human brain. J Neurosci. 29:727–742.

Gerbella M, Belmalih A, Borra E, Rozzi S, Luppino G. 2010. Cortical connections of the macaque caudal ventrolateral prefrontal areas 45A and 45B. Cereb Cortex. 20:141–168.

Gerbella M, Borra E, Tonelli S, Rozzi S, Luppino G. 2013. Connectional heterogeneity of the ventral part of the macaque area 46. Cereb Cortex. 23:967–987.

Geyer S, Luppino G, Rozzi S. 2012. Motor Cortex. In: Mai J,, Paxinos G, editors. The human nervous system. third. ed. Academic Press, Elsevier. p. 1012–1035.

Geyer S, Matelli M, Luppino G, Zilles K. 2000. Functional neuroanatomy of the primate isocortical motor system. Anat Embryol (Berl). 202:443–474.

Ghazanfar A a., Nielsen K, Logothetis NK. 2006. Eye movements of monkey observers viewing vocalizing conspecifics. Cognition. 101:515–529.

Ghaziri J, Tucholka A, Girard G, Houde JC, Boucher O, Gilbert G, Descoteaux M, Lippé S, Rainville P, Nguyen DK. 2017. The corticocortical structural connectivity of the human insula. Cereb Cortex. 27:1216–1228. doi: 10.1093/cercor/bhv308.

Goldenberg G, Spatt J. 2009. The neural basis of tool use. Brain. 132:1645–1655.

Grefkes C, Weiss PH, Zilles K, Fink GR. 2002. Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. Neuron. 35:173–184.

Gregoriou GG, Borra E, Matelli M, Luppino G. 2006. Architectonic organization of the inferior parietal convexity of the macaque monkey. J Comp Neurol. 496:422–451.

Grèzes J, Decety J. 2001. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum Brain Mapp. 12:1–19.

Grol MJ, Majdandzić J, Stephan KE, Verhagen L, Dijkerman HC, Bekkering H, Verstraten FA, Toni I. 2007. Parieto-frontal connectivity during visually guided grasping. J Neurosci. 27:11877–11887.

Grosbras M-H, Beaton S, Eickhoff SB. 2012. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. Hum Brain Mapp. 33:431–454.

Grosbras M-H, Laird AR, Paus T. 2005. Cortical regions involved in eye movements, shifts of attention, and gaze perception. Hum Brain Mapp. 25:140–154.

Haaland KY, Harrington DL, Knight RT. 2000. Neural representations of skilled movement. Brain. 123:2306–2313.

Hadland KA, Rushworth MF, Passingham RE, Jahanshahi M, Rothwell JC. 2001. Interference with performance of a response selection task that has no working memory component: an rTMS comparison of the dorsolateral prefrontal and medial frontal cortex. J Cogn Neurosci. 13:1097–1108.

Hasan A, Galea JM, Casula EP, Falkai P, Bestmann S, Rothwell JC. 2013. Muscle and timingspecific functional connectivity between the dorsolateral prefrontal cortex and the primary motor cortex. J Cogn Neurosci. 25:558–570.

Hecht EE, Gutman D a., Preuss TM, Sanchez MM, Parr L a., Rilling JK. 2013. Process versus product in social learning: Comparative diffusion tensor imaging of neural systems for action execution-observation matching in macaques, chimpanzees, and humans. Cereb Cortex. 23:1014–1024.

Heide W, Binkofski F, Seitz RJ, Posse S, Nitschke MF, Freund HJ, Kömpf D. 2001. Activation of frontoparietal cortices during memorized triple-step sequences of saccadic eye movements: an fMRI study. Eur J Neurosci. 13:1177–1189.

Herculano-Houzel S. 2009. The human brain in numbers: a linearly scaled-up primate brain. Front Hum Neurosci. 3:1–11.

Higuchi S, Holle H, Roberts N, Eickhoff SB, Vogt S. 2012. Imitation and observational learning of hand actions: prefrontal involvement and connectivity. Neuroimage. 59:1668–1683.

Hihara S, Taoka M, Tanaka M, Iriki A. 2015. Visual responsiveness of neurons in the secondary somatosensory area and its surrounding parietal operculum regions in awake macaque monkeys. Cereb Cortex. 25:1–16.

Hill J, Inder T, Neil J, Dierker D, Harwell J, Van Essen D. 2010. Similar patterns of cortical expansion during human development and evolution. Proc Natl Acad Sci. 107:13135–13140.

Hinkley LB, Krubitzer LA, Nagarajan SS, Disbrow E a. 2007. Sensorimotor integration in S2, PV, and parietal rostroventral areas of the human sylvian fissure. J Neurophysiol. 97:1288–1297.

Hooker CI, Paller KA, Gitelman DR, Parrish TB, Mesulam M-M, Reber PJ. 2003. Brain networks for analyzing eye gaze. Brain Res Cogn Brain Res. 17:406–418.

Hoshi E, Shima K, Tanji J. 1998. Task-dependent selectivity of movement-related neuronal activity in the primate prefrontal cortex. J Neurophysiol. 80:3392–3397.

Hoshi E, Shima K, Tanji J. 2000. Neuronal activity in the primate prefrontal cortex in the process of motor selection based on two behavioral rules. J Neurophysiol. 83:2355–2373.

Huerta MF, Kaas JH. 1990. Supplementary eye field as defined by intracortical microstimulation: connections in macaques. J Comp Neurol. 293:299–330.

Huerta MF, Krubitzer LA, Kaas JH. 1987. Frontal eye field as defined by intracortical microstimulation in squirrel monkeys, owl monkeys, and macaque monkeys II. cortical connections. J Comp Neurol. 265:332–361.

Ibañez A, Gleichgerrcht E, Manes F. 2010. Clinical effects of insular damage in humans. Brain Struct Funct. 214:397–410.

Ichihara-Takeda S, Funahashi S. 2007. Activity of primate orbitofrontal and dorsolateral prefrontal neurons: task-related activity during an oculomotor delayed-response task. Exp brain Res. 181:409–425.

James TW, Humphrey GK, Gati JS, Servos P, Menon RS, Goodale MA. 2002. Haptic study of three-dimensional objects activates extrastriate visual areas. Neuropsychologia. 40:1706–1714.

Jastorff J, Orban GA. 2009. Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing. J Neurosci. 29:7315–7329.

Jeannerod M, Arbib M a., Rizzolatti G, Sakata H. 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci. 18:314–320.

Jellema T, Baker CII, Wicker B, Perrett DII. 2000. Neural representation for the perception of the intentionality of actions. Brain Cogn. 44:280–302.

Jellema T, Perrett DI. 2003. Perceptual history influences neural responses to face and body postures. J Cogn Neurosci. 15:961–971.

Jenmalm P, Schmitz C, Forssberg H, Ehrsson HH. 2006. Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. J Neurosci. 26:9015–9021.

Jezzini A, Caruana F, Stoianov I, Gallese V, Rizzolatti G. 2012. Functional organization of the insula and inner perisylvian regions. Proc Natl Acad Sci U S A. 109:10077–10082.

Johnson-Frey SH. 2004. The neural bases of complex tool use in humans. Trends Cogn Sci. 8:71–78.

Johnson-Frey SH, Newman-Norlund R, Grafton ST. 2005. A distributed left hemisphere network active during planning of everyday tool use skills. Cereb cortex. 15:681–695.

Kaas JH, Stepniewska I. 2016. Evolution of posterior parietal cortex and parietal-frontal networks for specific actions in primates. J Comp Neurol. 524:595–608.

Kamali A, Sair HI, Radmanesh A, Hasan KM. 2014. Decoding the superior parietal lobule connections of the superior longitudinal fasciculus/arcuate fasciculus in the human brain. Neuroscience. 277:577–583.

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci. 17:4302–4311.

Klaes C, Kellis S, Aflalo T, Lee B, Pejsa K, Shanfield K, Hayes-Jackson S, Aisen M, Heck C, Liu C, Andersen RA. 2015. Hand shape representations in the human posterior parietal cortex. J Neurosci. 35:15466–15476.

Koyama M, Hasegawa I, Osada T, Adachi Y, Nakahara K, Miyashita Y. 2004. Functional magnetic resonance imaging of macaque monkeys performing visually guided saccade tasks:

comparison of cortical eye fields with humans. Neuron. 41:795–807.

Kuraoka K, Konoike N, Nakamura K. 2015. Functional differences in face processing between the amygdala and ventrolateral prefrontal cortex in monkeys. Neuroscience. 304:71–80.

Lacey S, Flueckiger P, Stilla R, Lava M, Sathian K. 2010. Object familiarity modulates the relationship between visual object imagery and haptic shape perception. Neuroimage. 49:1977–1990.

Lacey S, Tal N, Amedi A, Sathian K. 2009. A putative model of multisensory object representation. Brain Topogr. 21:269–274.

Luna B, Thulborn KR, Strojwas MH, McCurtain BJ, Berman RA, Genovese CR, Sweeney JA. 1998. Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. Cereb cortex. 8:40–47.

Luppino G, Calzavara R, Rozzi S, Matelli M. 2001. Projections from the superior temporal sulcus to the agranular frontal cortex in the macaque. Eur J Neurosci. 14:1035–1040.

Lynch JC, Tian JR. 2006. Cortico-cortical networks and cortico-subcortical loops for the higher control of eye movements. Prog Brain Res. 151:461–501.

Mahon BZ, Milleville SC, Negri G a L, Rumiati RI, Caramazza A, Martin A. 2007. Action-related properties shape object representations in the ventral stream. Neuron. 55:507–520.

Makris N, Kennedy DN, McInerney S, Sorensen AG, Wang R, Caviness VS, Pandya DN. 2005. Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. Cereb Cortex. 15:854–869.

Makris N, Papadimitriou GM, Kaiser JR, Sorg S, Kennedy DN, Pandya DN. 2009. Delineation of the middle longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. Cereb Cortex. 19:777–785.

Makris N, Preti MG, Asami T, Pelavin P, Campbell B, Papadimitriou GM, Kaiser J, Baselli G, Westin CF, Shenton ME, Kubicki M. 2013. Human middle longitudinal fascicle: variations in patterns of anatomical connections. Brain Struct Funct. 218:951–968.

Makris N, Zhu A, Papadimitriou GM, Mouradian P, Ng I. 2016. Mapping temporo-parietal and temporo-occipital cortico-cortical connections of the human middle longitudinal fascicle in subject-specific, probabilistic, and stereotaxic Talairach spaces.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci U S A. 92:8135–8139.

Mantini D, Corbetta M, Romani GL, Orban GA., Vanduffel W. 2013. Evolutionarily novel functional networks in the human brain? J Neurosci. 33:3259–3275.

Marquardt K, Ramezanpour H, Dicke PW, Thier P. 2017. Following eye gaze activates a patch in the posterior temporal cortex that is not part of the human “face patch” system. eneuro. 4:ENEURO.0317-16.2017.

Martino J, da Silva-Freitas R, Caballero H, Marco de Lucas E, García-Porrero JA, Vázquez-Barquero A. 2013. Fiber dissection and diffusion tensor imaging tractography study of the temporoparietal fiber intersection area. Neurosurgery. 72:87-97-8.

Maule F, Barchiesi G, Brochier T, Cattaneo L. 2015. Haptic working memory for grasping: the role of the parietal operculum. Cereb Cortex. 25:528–537.

Mistlin AJ, Perrett DI. 1990. Visual and somatosensory processing in the macaque temporal cortex: the role of “expectation”. Exp brain Res. 82:437–450.

Molenberghs P, Sale M V, Mattingley JB. 2012. Is there a critical lesion site for unilateral spatial neglect? A meta-analysis using activation likelihood estimation. Front Hum Neurosci. 6:78. doi: 10.3389/fnhum.2012.00078.

Moll J, de Oliveira-Souza R, Passman LJ, Cunha FC, Souza-Lima F, Andreiuolo PA. 2000. Functional MRI correlates of real and imagined tool-use pantomimes. Neurology. 54:1331–1336.

Monaco S, Sedda A, Cavina-Pratesi C, Culham JC. 2015. Neural correlates of object size and object location during grasping actions. Eur J Neurosci. 41:454–465.

Mort DJ, Perry RJ, Mannan SK, Hodgson TL, Anderson E, Quest R, McRobbie D, McBride A, Husain M, Kennard C. 2003. Differential cortical activation during voluntary and reflexive saccades in man. Neuroimage. 18:231–246.

Moschovakis AK, Gregoriou GG, Ugolini G, Doldan M, Graf W, Guldin W, Hadjidimitrakis K, Savaki HE. 2004. Oculomotor areas of the primate frontal lobes: a transneuronal transfer of rabies virus and [14C]-2-deoxyglucose functional imaging study. J Neurosci. 24:5726–5740.

Nachev P, Kennard C, Husain M. 2008. Functional role of the supplementary and pre-supplementary motor areas. Nat Rev Neurosci. 9:856–869.

Nelissen K, Borra E, Gerbella M, Rozzi S, Luppino G, Vanduffel W, Rizzolatti G, Orban GA. 2011. Action observation circuits in the macaque monkey cortex. J Neurosci. 31:3743–3756.

Nelissen K, Luppino G, Vanduffel W, Rizzolatti G, Orban GA. 2005. Observing others: multiple action representation in the frontal lobe. Science. 310:332–336.

Nummenmaa L, Calder AJ. 2009. Neural mechanisms of social attention. Trends Cogn Sci. 13:135–143.

Orban GA. 2016. Functional definitions of parietal areas in human and non-human primates. Proc Biol Sci. 283. doi: 10.1098/rspb.2016.0118

Orban GA, Caruana F. 2014. The neural basis of human tool use. Front Psychol. 5:1–12.

Orban GA, Van Essen D, Vanduffel W. 2004. Comparative mapping of higher visual areas in monkeys and humans. Trends Cogn Sci. 8:315–324.

Orban GA, Zhu Q, Vanduffel W. 2014. The transition in the ventral stream from feature to real-world entity representations. Front Psychol. 5:1–9.

Passingham R. 2009. How good is the macaque monkey model of the human brain? Curr Opin Neurobiol. 19:6–11.

Patel GH, Yang D, Jamerson EC, Snyder LH, Corbetta M, Ferrera VP. 2015. Functional evolution of new and expanded attention networks in humans. Proc Natl Acad Sci U S A. 112:9454–9459.

Peelen MV, Bracci S, Lu X, He C, Caramazza A, Bi Y. 2013. Tool selectivity in left occipitotemporal cortex develops without vision. J Cogn Neurosci. 25:1225–1234.

Peeters RR, Rizzolatti G, Orban GA. 2013. Functional properties of the left parietal tool use region. Neuroimage. 78:83–93.

Peeters RR, Simone L, Nelissen K, Fabbri-Destro M, Vanduffel W, Rizzolatti G, Orban GA. 2009. The representation of tool use in humans and monkeys: common and uniquely human features. J Neurosci. 29:11523–11539.

Peng X, Sereno ME, Silva AK, Lehky SR, Sereno AB. 2008. Shape selectivity in primate frontal eye field. J Neurophysiol. 100:796–814.

Penn DC, Holyoak KJ, Povinelli DJ. 2008. Darwin’s mistake: explaining the discontinuity between human and nonhuman minds. Behav Brain Sci. 31:109–130.

Petit L, Clark VP, Ingeholm J, Haxby JV. 1997. Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. J Neurophysiol. 77:3386–3390.

Petit L, Haxby JV. 1999. Functional anatomy of pursuit eye movements in humans as revealed by fMRI. J Neurophysiol. 82:463–471.

Petrides M. 2005. Lateral prefrontal cortex: architectonic and functional organization. Philos Trans R Soc Lond B Biol Sci. 360:781–795.

Picard N, Strick PL. 1996. Motor areas of the medial wall: a review of their location and functional activation. Cereb Cortex. 6:342–353.

Picard N, Strick PL. 2001. Imaging the premotor areas. Curr Opin Neurobiol. 11:663–672.

Prabhu G, Shimazu H, Cerri G, Brochier T, Spinks RL, Maier MA, Lemon RN. 2009. Modulation of primary motor cortex outputs from ventral premotor cortex during visually guided grasp in the macaque monkey. J Physiol. 587:1057–1069.

Premereur E, Janssen P, Vanduffel W. 2015. Effector specificity in macaque frontal and parietal cortex. J Neurosci. 35:3446–3459.

Preston TJ, Guo F, Das K, Giesbrecht B, Eckstein MP. 2013. Neural representations of contextual guidance in visual search of real-world scenes. J Neurosci. 33:7846–7855.

Preuss TM. 2011. The human brain: rewired and running hot. Ann N Y Acad Sci. 1225:182–191.

Pulvermüller F, 2018. Neural reuse of action perception circuits for language, concepts and communication. Progress in Neurobiology 160:1–44.

Ramayya AG, Glasser MF, Rilling JK. 2010. A DTI investigation of neural substrates supporting tool use. Cereb Cortex. 20:507–516.

Reed CL, Shoham S, Halgren E. 2004. Neural substrates of tactile object recognition: an fMRI study. Hum Brain Mapp. 21:236–246.

Requin J, Lecas JC, Vitton N. 1990. A comparison of preparation-related neuronal activity changes in the prefrontal, premotor, primary motor and posterior parietal areas of the monkey cortex: preliminary results. Neurosci Lett. 111:151–156.

Reveley C, Seth AK, Pierpaoli C, Silva AC, Yu D, Saunders RC, Leopold DA, Ye FQ. 2015. Superficial white matter fiber systems impede detection of long-range cortical connections in diffusion MR tractography. Proc Natl Acad Sci. 112:E2820–E2828.

Rice NJ, Tunik E, Grafton ST. 2006. The anterior intraparietal sulcus mediates grasp execution, independent of requirement to update: new insights from transcranial magnetic stimulation. J Neurosci. 26:8176–8182.

Ridderinkhof RK, Forstmann BU, Wylie SA, Burle B, van den Wildenberg WPM. 2011. Neurocognitive mechanisms of action control: resisting the call of the Sirens. Wiley Interdiscip Rev Cogn Sci. 2:174–192.

Rilling JK, Glasser MF, Jbabdi S, Andersson J, Preuss TM. 2012. Continuity, divergence, and the evolution of brain language pathways. Front Evol Neurosci. 3:11.

Rilling JK, Glasser MF, Preuss TM, Ma X, Zhao T, Hu X, Behrens TEJ. 2008. The evolution of the arcuate fasciculus revealed with comparative DTI. Nat Neurosci. 11:426–428.

Rizzolatti G, Arbib MA. 1998. Language within our grasp. Trends Neurosci. 21:188–194.

Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S. 2014. Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. Physiol Rev. 94:655–706.

Rizzolatti G, Fadiga L, Gallese V, Fogassi L. 1996. Premotor cortex and the recognition of motor actions. Brain Res Cogn Brain Res. 3:131–141.

Rizzolatti G, Luppino G. 2001. The cortical motor system. Neuron. 31:889–901.

Rojkova K, Volle E, Urbanski M, Humbert F, Dell'Acqua F, Thiebaut de Schotten M. 2016.

Atlasing the frontal lobe connections and their variability due to age and education: a spherical deconvolution tractography study. Brain Struct Funct. 221:1751–66. doi: 10.1007/s00429-015-1001-3.

Romanski LM, Averbeck BB. 2009. The primate cortical auditory system and neural representation of conspecific vocalizations. Annu Rev Neurosci. 32:315–346.

Rosano C, Krisky CM, Welling JS, Eddy WF, Luna B, Thulborn KR, Sweeney JA. 2002. Pursuit and saccadic eye movement subregions in human frontal eye field: a high-resolution fMRI investigation. Cereb Cortex. 12:107–115.

Rosano C, Sweeney JA, Melchitzky DS, Lewis DA. 2003. The human precentral sulcus: chemoarchitecture of a region corresponding to the frontal eye fields. Brain Res. 972:16–30.

Rowe JB, Stephan KE, Friston K, Frackowiak RSJ, Passingham RE. 2005. The prefrontal cortex shows context-specific changes in effective connectivity to motor or visual cortex during the selection of action or colour. Cereb Cortex. 15:85–95.

Roy A, Shepherd S V, Platt ML. 2014. Reversible inactivation of pSTS suppresses social gaze following in the macaque (Macaca mulatta). Soc Cogn Affect Neurosci. 9:209–217.

Rozzi S, Calzavara R, Belmalih A, Borra E, Gregoriou GG, Matelli M, Luppino G. 2006. Cortical connections of the inferior parietal cortical convexity of the macaque monkey. Cereb Cortex. 16:1389–1417.

Rozzi S, Ferrari PF, Bonini L, Rizzolatti G, Fogassi L. 2008. Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. Eur J Neurosci. 28:1569–1588.

Ruschel M, Knösche TR, Friederici AD, Turner R, Geyer S, Anwander A. 2014. Connectivity architecture and subdivision of the human inferior parietal cortex revealed by diffusion MRI. Cereb Cortex. 24:2436–2448.

Rushworth MFS, Behrens TEJ, Johansen-Berg H. 2006. Connection patterns distinguish 3 regions of human parietal cortex. Cereb Cortex. 16:1418–1430.

Sakata H, Taira M, Kusunoki M, Murata A, Tanaka Y. 1997. The TINS lecture: The parietal association cortex in depth perception and visual control of hand action. Trends Neurosci. 20:350–357.

Saleem KS, Miller B, Price JL. 2014. Subdivisions and connectional networks of the lateral prefrontal cortex in the macaque monkey. J Comp Neurol. 522:1641–1690.

Sarubbo S, De Benedictis A, Maldonado IL, Basso G, Duffau H. 2013. Frontal terminations for the inferior fronto-occipital fascicle: anatomical dissection, DTI study and functional considerations on a multi-component bundle. Brain Struct Funct. 218:21–37.

Savini N, Babiloni C, Brunetti M, Caulo M, Del Gratta C, Perrucci MG, Rossini PM, Romani GL, Ferretti A. 2010. Passive tactile recognition of geometrical shape in humans: an fMRI study. Brain Res Bull. 83:223–231.

Schall JD, Morel A, King DJ, Bullier J. 1995. Topography of visual cortex connections with frontal eye field in macaque: convergence and segregation of processing streams. J Neurosci. 15:4464–4487.

Scheperjans F, Hermann K, Eickhoff SB, Amunts K, Schleicher A, Zilles K. 2008. Observer-independent cytoarchitectonic mapping of the human superior parietal cortex. Cereb Cortex. 18:846–867.

Schmahmann JD, Pandya DN, Wang R, Dai G, D'Arceuil HE, De Crespigny AJ, Wedeen VJ. 2007. Association fibre pathways of the brain: parallel observations from diffusion spectrum imaging and autoradiography. Brain. 130:630–653.

Schubotz RI, Anwander A, Knösche TR, von Cramon DY, Tittgemeyer M. 2010. Anatomical and functional parcellation of the human lateral premotor cortex. Neuroimage. 50:396–408.

Semendeferi K, Lu A, Schenker N, Damasio H. 2002. Humans and great apes share a large frontal cortex. Nat Neurosci. 5:272–276.

Sereno AB, Maunsell JH. 1998. Shape selectivity in primate lateral intraparietal cortex. Nature. 395:500–503.

Sereno MI, Tootell RB. 2005. From monkeys to humans: what do we now know about brain homologies? Curr Opin Neurobiol. 15:135–144.

Shepherd S V. 2010. Following gaze: gaze-following behavior as a window into social cognition. Front Integr Neurosci. 4:5.

Shepherd S V, Klein JT, Deaner RO, Platt ML. 2009. Mirroring of attention by neurons in macaque parietal cortex. Proc Natl Acad Sci U S A. 106:9489–9494.

Sherwood CC, Subiaul F, Zawidzki TW. 2008. A natural history of the human mind: Tracing evolutionary changes in brain and cognition. J Anat. 212:426–454.

Shikata E, Hamzei F, Glauche V, Koch M, Weiller C, Binkofski F, Büchel C. 2003. Functional properties and interaction of the anterior and posterior intraparietal areas in humans. Eur J Neurosci. 17:1105–1110.

Shimazu H, Maier MA, Cerri G, Kirkwood P a, Lemon RN. 2004. Macaque ventral premotor cortex exerts powerful facilitation of motor cortex outputs to upper limb motoneurons. J Neurosci. 24:1200–1211.

Simone L, Bimbi M, Rodà F, Fogassi L, Rozzi S. 2017. Action observation activates neurons of the monkey ventrolateral prefrontal cortex. Sci Rep. 7:44378. doi: 10.1038/srep44378.

Simone L, Rozzi S, Bimbi M, Fogassi L. 2015. Movement-related activity during goal-directed hand actions in the monkey ventrolateral prefrontal cortex. Eur J Neurosci. 42:2882–2894.

Sporns O. 2013. Structure and function of complex brain networks. Dialogues Clin Neurosci. 15:247–62.

Stanton GB, Bruce CJ, Goldberg ME. 1993. Topography of projections to the frontal lobe from the macaque frontal eye fields. J Comp Neurol. 330:286–301.

Stanton GB, Bruce CJ, Goldberg ME. 1995. Topography of projections to posterior cortical areas from the macaque frontal eye fields. J Comp Neurol. 353:291–305.

Stylianou-Korsnes M, Reiner M, Magnussen SJ, Feldman MW. 2010. Visual recognition of shapes and textures: an fMRi study. Brain Struct Funct. 214:355–359.

Sugihara T, Diltz MD, Averbeck BB, Romanski LM. 2006. Integration of auditory and visual communication information in the primate ventrolateral prefrontal cortex. J Neurosci. 26:11138–11147.

Swann NC, Cai W, Conner CR, Pieters TA, Claffey MP, George JS, Aron AR, Tandon N. 2012. Roles for the pre-supplementary motor area and the right inferior frontal gyrus in stopping action: electrophysiological responses and functional and structural connectivity. Neuroimage. 59:2860–2870.

Tal N, Amedi A. 2009. Multisensory visual-tactile object related network in humans: insights gained using a novel crossmodal adaptation approach. Exp brain Res. 198:165–182.

Tanaka K. 1996. Representation of visual features of objects in the inferotemporal cortex. Neural Networks. 9:1459–1475.

Tanji J, Hoshi E. 2008. Role of the lateral prefrontal cortex in executive behavioral control. Physiol Rev. 88:37–57.

Thiebaut de Schotten M, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, Murphy DGM, Catani M. 2011. A lateralized brain network for visuospatial attention. Nat Neurosci. 14:1245–1246.

Thiebaut de Schotten M, Dell'Acqua F, Valabregue R, Catani M, Dell'Acqua F, Valabregue R. 2012. Monkey to human comparative anatomy of the frontal lobe association tracts. Cortex. 48:82–96.

Thomas C, Ye FQ, Irfanoglu MO, Modi P, Saleem KS, Leopold DA, Pierpaoli C. 2014. Anatomical accuracy of brain connections derived from diffusion MRI tractography is inherently limited. Proc Natl Acad Sci. 111:16574–16579.

Toni I, Rushworth MFS, Passingham RE. 2001. Neural correlates of visuomotor associations spatial rules compared with arbitrary rules. Exp Brain Res. 141:359–369.

Toth LJ, Assad JA. 2002. Dynamic coding of behaviourally relevant stimuli in parietal cortex. Nature. 415:165–168.

Tsao DY, Moeller S, Freiwald WA. 2008a. Comparing face patch systems in macaques and humans. Proc Natl Acad Sci U S A. 105:19514-9. doi: 10.1073/pnas.0809662105.

Tsao DY, Schweers N, Moeller S, Freiwald WA. 2008b. Patches of face-selective cortex in the macaque frontal lobe. Nat Neurosci. 11:877–879.

Tunik E, Frey SH, Grafton ST. 2005. Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. Nat Neurosci. 8:505–511.

Tunik E, Lo O-Y, Adamovich S V. 2008. Transcranial magnetic stimulation to the frontal operculum and supramarginal gyrus disrupts planning of outcome-based hand-object interactions. J Neurosci. 28:14422–14427.

Umilta MA, Brochier T, Spinks RL, Lemon RN. 2007. Simultaneous recording of macaque premotor and primary motor cortex neuronal populations reveals different functional contributions to visuomotor grasp. J Neurophysiol. 98:488–501.

Van Essen DC. 1985. Functional organization of the primate visual cortex. In: Jones E,, Peters A, editors. Cerebral Cortex. New York: Plenum Press. p. 259–329.

van Polanen V, Davare M. 2015. Interactions between dorsal and ventral streams for controlling skilled grasp. Neuropsychologia. 79:186–91. doi: 10.1016/j.neuropsychologia.2015.07.010.

Verhagen L, Dijkerman HC, Grol MJ, Toni I. 2008. Perceptuo-motor interactions during prehension movements. J Neurosci. 28:4726–4735.

Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, Eickhoff SB, Freund HJ, Rizzolatti G, Fink GR. 2007. Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage. 37:1371–1383.

Wang Y, Fernández-Miranda JC, Verstynen T, Pathak S, Schneider W, Yeh F-C. 2013. Rethinking the role of the middle longitudinal fascicle in language and auditory pathways. Cereb Cortex. 23:2347–2356.

Ward MK, Bolding MS, Schultz KP, Gamlin PD. 2015. Mapping the macaque superior temporal sulcus: functional delineation of vergence and version eye-movement-related activity. J Neurosci. 35:7428–7442.

Wardak C, Olivier E, Duhamel J-R. 2011. The relationship between spatial attention and saccades in the frontoparietal network of the monkey. Eur J Neurosci. 33:1973–1981.

Wardak C, Vanduffel W, Orban GA. 2010. Searching for a salient target involves frontal regions. Cereb Cortex. 20:2464–2477.

Williams JHG, Waiter GD, Perra O, Perrett DI, Whiten A. 2005. An fMRI study of joint attention experience. Neuroimage. 25:133–140.

Wu Y, Sun D, Wang Y, Wang Y, Wang Y. 2016. Tracing short connections of the temporo-parieto-occipital region in the human brain using diffusion spectrum imaging and fiber dissection. Brain Res. 1646:152–159.

Yoshida K, Saito N, Iriki A, Isoda M. 2011. Representation of others' action by neurons in monkey medial frontal cortex. Curr Biol. 21:249–253.

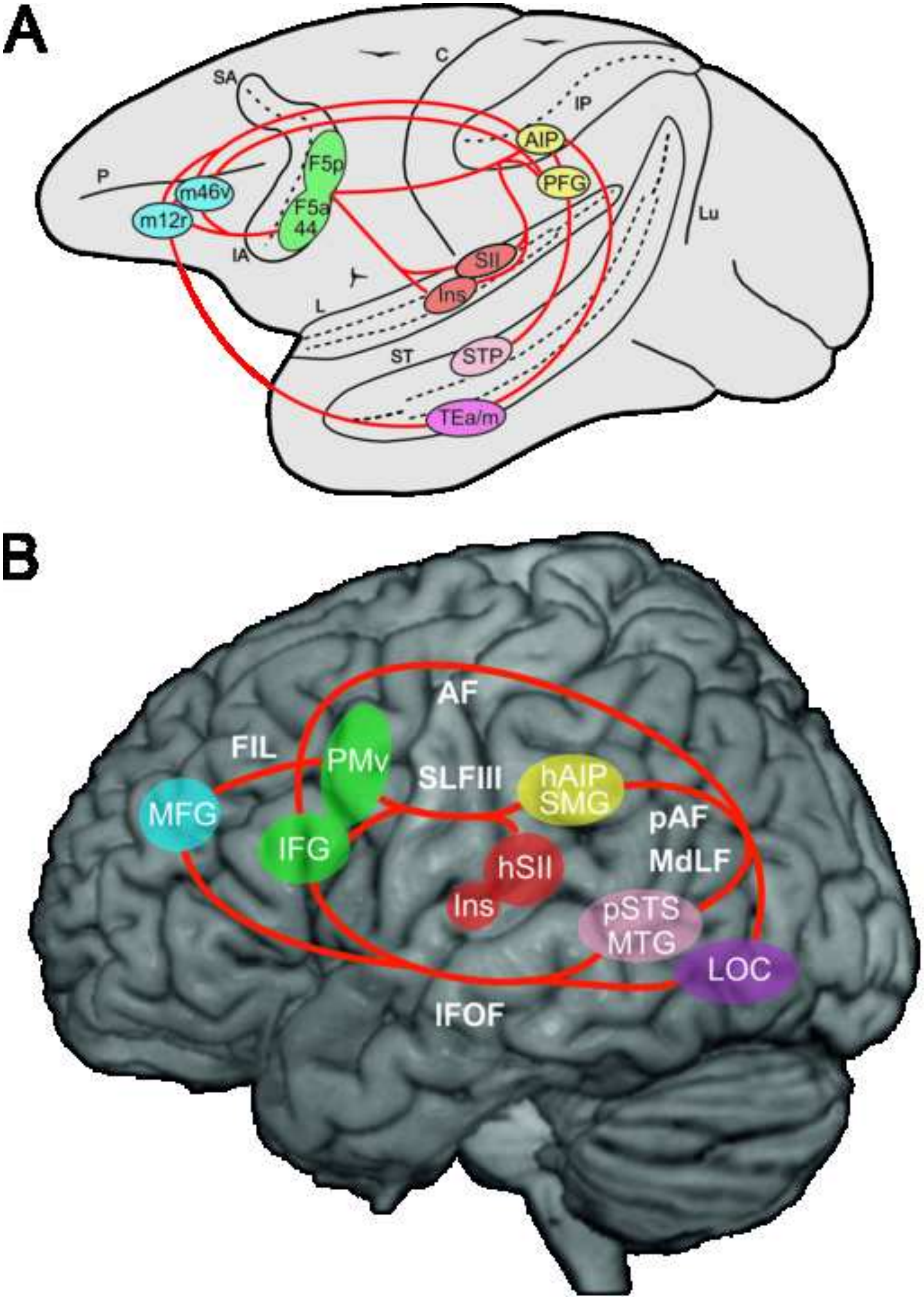
Yoshida K, Saito N, Iriki A, Isoda M. 2012. Social error monitoring in macaque frontal cortex. Nat Neurosci. 15:1307–1312.

Zilles K, Schlaug G, Geyer S, Luppino G, Matelli M, Qü M, Schleicher A, Schormann T. 1996. Anatomy and transmitter receptors of the supplementary motor areas in the human and nonhuman primate brain. Adv Neurol. 70:29–43.

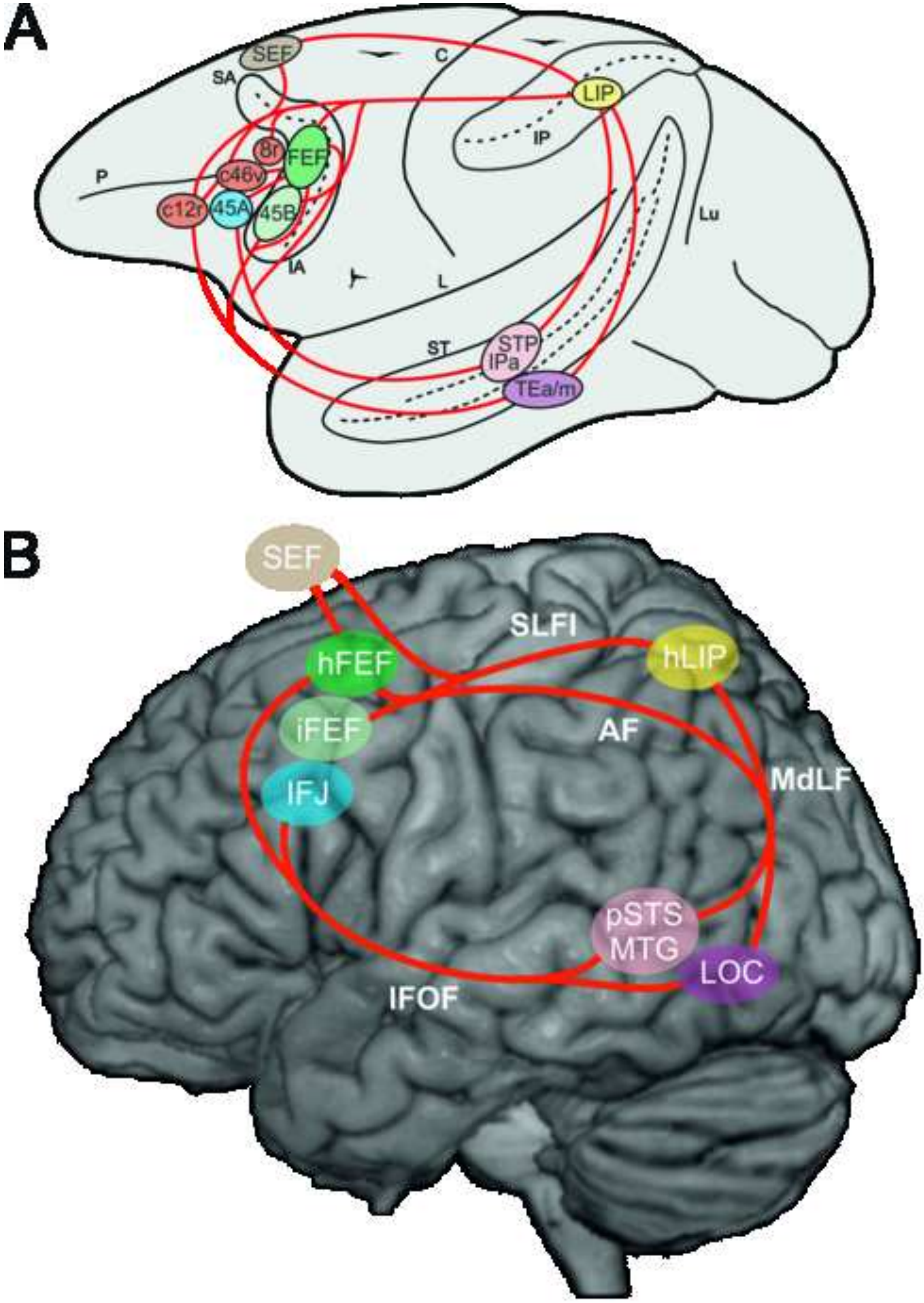
Figure legends

Figure 1. The macaque lateral grasping/action recognition network and its possible human counterpart. **(A)** Lateral view of an hemisphere of the macaque brain showing the main nodes of the lateral grasping/action observation network and their interconnections defined based on tract tracing connectional data. C = central sulcus; IA = inferior arcuate sulcus; IP = intraparietal sulcus; L = lateral sulcus; Lu = lunate sulcus; m12r = middle part of area 12r; m46v = middle part of area 46v; P = principal sulcus; ST = superior temporal sulcus. **(B)** Lateral view of an hemisphere of the human brain showing with the same color the possible homologues of the main nodes of the macaque lateral grasping/action observation network and their possible interconnections based on dMRI data. AF = Arcuate fasciculus; FIL = Frontal inferior longitudinal tract; hAIP = Human anterior intraparietal area; hSII = Human second somatosensory area; IFG = Inferior frontal gyrus; IFOF = Inferior fronto-occipital fasciculus; Ins = Insula; LOC = Lateral occipital complex; MdLF = Middle longitudinal fasciculus; MFG = Middle frontal gyrus; MTG = Middle temporal gyrus; pAF = Posterior segment of the arcuate fasciculus; PMv = Ventral premotor cortex; pSTS = Posterior superior temporal sulcus; SLFIII = Third branch of the superior longitudinal fasciculus; SMG = Supramarginal gyrys;

Figure 2. The macaque network for explorative and communicative oculomotor behavior and its possible human counterpart. **(A)** Lateral view of an hemisphere of the macaque brain showing the main nodes of the explorative and communicative oculomotor network and their interconnections defined based on tract tracing connectional data. Temporal connections of the SEF are not shown. c12r = caudal part of area 12r; c46v = caudal part of area 46v. Other abbreviations as in Figure 1. **(B)** Lateral view of an hemisphere of the human brain showing with the same color the possible homologues of the main nodes of the macaque explorative and communicative oculomotor network and their possible interconnections based on dMRI data. The Supplementary Eye Field (SEF) is located on in the medial wall of the hemisphere. hFEF = Human frontal eye field; hLIP = Human lateral intraparietal area; iFEF = Inferior frontal eye field; IFJ = Inferior frontal junction; SLFI = First branch of the superior longitudinal fasciculus. Other abbreviations as in Figure 1.


A
C
SA
IP
AIP
F5p
PFG
P
m46v
m12r
F5a
44
Lu
IA
SII
L
Ins
ST
STP
TEa/m
B
AF
FIL
PMv
SLFIII
hAIP
SMG
MFG
IFG
pAF
hSII
MdLF
Ins
pSTS
MTG
LOC
IFOF

Figure


A
SEF
SA
C
LIP
IP
8r
FEF
P
c46v
c12r
45A
45B
IA
L
Lu
ST
STP
IPa
TEa/m
B
SEF
SLFI
hFEF
hLIP
iFEF
AF
MdLF
IFJ
pSTS
MTG
LOC
IFOF