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Functional anatomy of the macaque temporo-parieto-frontal connectivity.

This is the peer reviewed version of the following article:

Original

Functional anatomy of the macaque temporo-parieto-frontal connectivity / Borra, Elena; Luppino, Giuseppe. - In: CORTEX. - ISSN 0010-9452. - 97:(2017), pp. 306-326. [10.1016/j.cortex.2016.12.007]

Availability:

This version is available at: 11381/2822867 since: 2021-10-27T12:11:44Z

Publisher:

Masson SpA

Published

DOI:10.1016/j.cortex.2016.12.007

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note finali coverpage

(Article begins on next page)

04 May 2024

Manuscript Number: CORTEX-D-16-00546R1

Title: Functional anatomy of the macaque temporo-parieto-frontal connectivity

Article Type: Review

Keywords: parietal cortex; temporal cortex; inferior parietal lobule; motor control; sensorimotor transformations

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Abstract: The primate parietal lobe is primarily dedicated to the processing of sensory information for the guidance of motor behavior, based on the integration of sensory with motor signals (sensorimotor transformations), mediated by specific, strong, and reciprocal connections with the motor cortex. Sensorimotor transformations have been regarded as an automatic process carried out independently from the temporal cortex, which is considered the location where sensory information is used for perceptual processes. However, both human and non-human primate studies have shown interactions between these two regions in different aspects of sensorimotor and cognitive processes. Connectional studies in macaques have provided a detailed description of the possible neural substrate for these interactions. Specifically, temporo-parietal connections almost exclusively involve the inferior parietal lobule (IPL) and display a fine topographic organization, providing the substrate for the role of the macaque IPL in "perception-based" control of motor behavior. Particularly, more rostral IPL areas are involved in motor and cognitive motor functions related to hand action organization and oculomotor control as well as in action and intention understanding, whereas more caudal IPL areas are involved in multisensory integration for the construction of space representations for guiding arm and eye motor behavior. Temporal and IPL-interconnected areas also share connections with specific ventral frontal areas and are thus part of large-scale cortical networks in which the various nodes are linked through "dorsal" temporo-parieto-frontal and "ventral" temporo-frontal pathways. Anatomical and functional studies suggest homologies between human and macaque temporo-parieto-frontal connectivity; they also suggest that higher-order functions of the human IPL could have evolved from the exploitation and adaptation of phylogenetically older neural mechanisms that occur in macaque brains. Thus, connectional data from macaque studies appear essential for understanding human brain mechanisms, even in cases of cognitive abilities undeveloped in other animals, and for interpreting clinical data, including disconnection syndromes.



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Dear Dr. Catani,

Dear Dr. Ross,

We are herewith submitting a revised version of the manuscript “Functional anatomy of the macaque temporo-parieto-frontal connectivity” for publication in the forthcoming Cortex Special Issue dedicated to the temporal and parietal lobes.

In revising the manuscript, all the comments and suggestions of the reviewers have been carefully taken into account. Accordingly, the title and abstract have been modified in order to make them more congruent with the coverage of the article and several changes have been made throughout the manuscript. Furthermore, a new figure has been added and the manuscript has been revised by a professional company for editing and proofreading.

In the Response to Reviewers 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 review article can be considered acceptable for publication in Cortex.

Sincerely yours,

Giuseppe Luppino

Functional anatomy of the macaque temporo-parieto-frontal connectivity

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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 the coverage of the topic of the present review and for highlighting some aspects that were underestimated in the previous version.

The following is the detailed description of the way in which the comments of the Reviewers have been addressed.

Reviewer #1:

Comment

The manuscript is well researched, with detailed description of the anatomy and very clear useful figures, however I feel the title and abstract do not fully reflect what is covered in the review. A notable example is that almost as much time is devoted to describing the role of the parieto-frontal connections as does the temporo-parietal connections, although this is hardly mentioned in the title, abstract or introduction.

Response

We agree with the Reviewer. The description of the functional anatomy of the parieto-frontal connectivity was necessary for the functional interpretation of the temporo-parietal connections and their involvement in large-scale cortical networks. However, it is true that the resulting coverage of the manuscript was not fully congruent with the title and abstract. Accordingly, we have modified the title and substantially modified the abstract.

Comment

The section on the human homologues is thin: it focuses mainly on homologous brain regions rather than connectivity per se. An example of this is page 18, line 55, whereby two possible white matter pathways are described as being homologous, yet no detail is given (for example the acronym MLF is not explained or expanded anywhere in the text).

Response

This section has been revised and slightly expanded in order to provide more details on the temporo-parietal connectivity of the human brain and on the possible homologies with the corresponding connectivity of the macaque brain.

Minor Comments

The English does not flow well throughout - it should be rechecked by a native English speaker.

Response

The manuscript has been revised by a professional company

Whilst the figures are generally clear and provide very useful guidance, it might be beneficial to add a figure showing possible homologous connections in humans.

Response

We have added a figure showing examples of large-scale cortical networks of the human brain, possibly evolved from phylogenetically older networks well characterized in the macaque brain.

Reviewer #2:

Comment

The paper's introduction, although thorough in providing a background on monkey connectivity studies, does not justify the central theme of the review. Why temporo-parietal connectivity? What is the gap/need in the literature to justify the review?

Response

In revising the manuscript we tried to declare more clearly the theme and aims of the present review article. This review, based on studies carried out mostly in the last decade, is to our knowledge the first in providing a comprehensive overview of the organization of the macaque temporo-parieto-frontal connectivity from the perspective of its specificity, participation to large-scale cortical networks, and possible homologies with the corresponding connectivity of the human brain.

Comment

This review provides little information on the methodological issues of the studies mentioned, or how the connectivity debate has evolved over the years. There is no critique on how studies limitations have or have not been addressed by other authors. Similarly, the concluding remarks do not offer an insight into future directions for the comparative field, and what important questions remain outstanding. This makes the paper largely read like a textbook.

Response

The aim of this review was to describe the temporo-parieto-frontal connectivity of the macaque brain and to argue that these data can be helpful for understanding the neural mechanisms underlying some high order functions of the human brain. Methodological issues have been addressed in this article (more in detail in the present revised version) only to note that non-invasive functional and connectional approaches used for studying the human brain still have technical limitations in terms of specificity and spatial resolution of the data, compared to the functional and connectional approaches that can be used in non-human primates. The last Section of the manuscript has been revised.

Minor comments:

- The title of the paper suggests a review on macaque temporo-parietal connectivity, when in fact, it also offers a broad review on overall parietal regions and connections associated with the fronto-parietal network and the dorsal and ventral streams. Perhaps a more encompassing title would prevent any confusion.

Response

We agree with the comment of the Reviewer. The Title (and Abstract) has been changed.

- Introduction, at the end of the second paragraph: "recent comparative studies in macaques have questioned its validity for precise in vivo tracing of point-to-point connectivity" - it's a vague statement and does not instruct the reader on what aspects of in-vivo tracing validity this could be referring to. This needs to be expanded a little more, regardless of providing references.

Response

The second paragraph of the Introduction has been revised and expanded in order to provide more details on the limitations of non-invasive MR-based approaches in studying brain connectivity.

- Introduction, the beginning of the 3rd paragraph states: "In this context, old world monkeys, such as macaques, are the primates most closely related to humans...", however it is not clear from the paragraph above, what exact context this is referring to. Also, does this statement refer to brain organisation or genetics? The paragraph needs to provide a background on why old world monkeys are the primates most closely related to humans (e.g. Kaas, 2013).

Response

This part of the Introduction (third-fifth paragraph) has been revised and reorganized also in order to eliminate some redundancies. In particular, we have specified that "Non-human primates such as macaques, are *the experimental model system phylogenetically closest to humans.....*".

- Introduction, 3rd paragraph, examples are given on the usefulness of monkey studies. References are missing after each example; multimodal architectonic studies, cortical maps, electrophysiological studies etc.

Response

We have provided some examples and references for these types of studies.

- The first sentence of the 4th paragraph on how non-human primates studies can be very helpful, is redundant, as this point has already been satisfactorily made.

Response

As mentioned above, this part of the introduction has been revised

- In section 2, " The macaque PPC", only the first paragraph is about the PPC, the second paragraph shifts to a description of parietal areas, which disrupts the flow. The descriptive anatomy should come first, then the subsections.

Response

The content of this Section has been reorganized

- In section 4, "The macaque temporal cortex", the 3rd paragraph briefly compares functional imaging studies in humans. The review thus far hasn't provided any comparisons to human studies, so this sentence seems out of place considering that other subsections don't follow this hierarchy.

Response

We fully agree with the Reviewer. Any reference to human studies in this Section was out of place and has been moved to Section 6.

- Section 6, page 19, "tool use" is discussed more than once in the same paragraph, which perhaps could be merged into one single point.

Response

This Section has been revised and reorganized. Tool use is now mentioned in only one paragraph (page 20).

Functional anatomy of the macaque temporo-parieto-frontal connectivity

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Abstract

The primate parietal lobe is primarily dedicated to the processing of sensory information for the guidance of motor behavior, based on the integration of sensory with motor signals (sensorimotor transformations), mediated by specific, strong, and reciprocal connections with the motor cortex. Sensorimotor transformations have been regarded as an automatic process carried out independently from the temporal cortex, which is considered the location where sensory information is used for perceptual processes. However, both human and non-human primate studies have shown interactions between these two regions in different aspects of sensorimotor and cognitive processes. Connectional studies in macaques have provided a detailed description of the possible neural substrate for these interactions. Specifically, temporo-parietal connections almost exclusively involve the inferior parietal lobule (IPL) and display a fine topographic organization, providing the substrate for the role of the macaque IPL in “perception-based” control of motor behavior. Particularly, more rostral IPL areas are involved in motor and cognitive motor functions related to hand action organization and oculomotor control as well as in action and intention understanding, whereas more caudal IPL areas are involved in multisensory integration for the construction of space representations for guiding arm and eye motor behavior. Temporal and IPL-interconnected areas also share connections with specific ventral frontal areas and are thus part of large-scale cortical networks in which the various nodes are linked through “dorsal” temporo-parieto-frontal and “ventral” temporo-frontal pathways. Anatomical and functional studies suggest homologies between human and macaque temporo-parieto-frontal connectivity; they also suggest that higher-order functions of the human IPL could have evolved from the exploitation and adaptation of phylogenetically older neural mechanisms that occur in macaque brains. Thus, connectional data from macaque studies appear essential for understanding human brain mechanisms, even in cases of cognitive abilities undeveloped in other animals, and for interpreting clinical data, including disconnection syndromes.

Keywords

parietal cortex; temporal cortex; inferior parietal lobule; motor control; sensorimotor transformations

1. Introduction

In neuroscience today, it is largely accepted that cortical functions are not confined to individual areas but result from the contribution of several, even distant, areas linked together by cortical connections and forming large-scale, functionally specialized networks (see, e.g., Catani et al., 2012). Accordingly, a full understanding of the neural mechanisms underlying a given cortical function also requires an anatomical definition of the underpinning neural substrate in terms of both the number and extent of areas potentially involved in that function and their cortical connectivity.

In recent years, the development of non-invasive functional and connectional imaging techniques has made it possible to address the issue of defining 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, intrinsic functional connectivity MRI (fcMRI) has recently emerged as a 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, the areal attribution of activation foci is at best based on probabilistic architectonic maps, which prevent univocal anatomo-functional correlations of experimental data. Second, recent studies of macaques in which well-known cortical pathways have been traced with dMRI have questioned the technique's validity for precise in vivo tracing of point-to-point connectivity (Reveley et al., 2015; Thomas et al., 2014). Indeed, these studies demonstrated that (i) an increase in the sensitivity of different methods seriously decreases specificity, and vice versa (Thomas et al., 2014); (ii) optimal parameters of the tractography algorithm vary according to the traced pathways (Thomas et al., 2014); and (iii) the complex arrangement of white matter fibers residing just under the cortical sheet poses severe challenges for long-range tractography (Reveley et al., 2015). 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 anatomic 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, Krienen, & Yeo, 2013).

Non-human primates such as macaques are the experimental model system phylogenetically closest to humans for obtaining highly detailed anatomical and functional information about the neural pathways and mechanisms underlying sensory, motor, and cognitive functions (see, e.g., Passingham, 2009; Sereno & Tootell, 2005). Indeed, based on comparative observations, it is

largely agreed that the monkey and human brain share a common plan of anatomical and functional organization of sensory, motor, and associated cortical areas (Caminiti, Innocenti, & Battaglia-Mayer, 2015; Geyer, Matelli, Luppino, & Zilles, 2000; Mantini, Corbetta, Romani, Orban, & Vanduffel, 2013; Orban, Van Essen, & Vanduffel, 2004).

In non-human primates, multimodal architectonic studies can provide reliable cortical maps that can be used as anatomical frames of reference for the univocal attribution of specific functional and connectional data, obtained in the same or different subjects, to specific cortical areas. Furthermore, electrophysiological studies can provide information on the functional properties of cortical areas, even at the level of individual neuronal activity. Finally, neural tracers, based on their anterograde and/or retrograde axonal transport, can provide information on the afferent and efferent connections of a given cortical sector at the cellular level and, via their laminar distribution, the hierarchical relationships between connected areas (see Felleman & Van Essen, 1991). These connectional data are crucial for assessing whether areas with common or similar functional properties belong to the same or different networks and to make hypotheses on the potential information flow through a given network. Thus, non-human primates provide invaluable data for building more comprehensive, anatomically plausible models of cortical functions, which could in turn be used for guiding anatomical and functional investigations in humans and supporting research-based clinical practices. For example, based on cyto-, myelo-, chemo-, and receptor-architectonic observations, the macaque inferior parietal convexity cortex has been subdivided into four different areas (Geyer, Luppino, Ekamp, & Zilles, 2005; Gregoriou, Borra, Matelli, & Luppino, 2006), which later studies have shown to be functionally and connectionally distinct (Rozzi et al., 2006; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008). These data have subsequently been used for suggesting homologies with the corresponding region of the human brain (Caspers et al., 2006, 2011, 2013).

One potential challenge to the generalization of non-human primate data to the human brain is that approximately 30 million years of independent evolution have resulted in significant differences between the brains of monkeys and humans; for example, compared to monkeys, a disproportionate enlargement of some cortical regions in the human brain is considered the neural basis for the outstanding cognitive capabilities of humans (see, e.g., Chaplin, Yu, Soares, Gattass, & Rosa, 2013; Passingham, 2009; Rilling, Glasser, Jbabdi, Andersson, & Preuss, 2012; Sereno & Tootell, 2005). However, it is largely accepted that similar features present in different members of a phylogenetic radiation can be explained as being retained from a common ancestor (see Kaas, 2013), and that evolutionary processes have more commonly involved the modification of existing anatomical structures than the addition of new ones. Thus, novel functions have mostly evolved from the adaptation of existing neural mechanisms (see, e.g., de Waal & Ferrari, 2010; Passingham,

2009; Rilling et al., 2012). The macaque model could thus be essential for understanding the mechanisms of the human brain, even those cognitive abilities that have not developed in other animals.

The general aim of this review article is to argue that this could also be the case for higher-order cognitive functions resulting from the interplay between the parietal, frontal, and temporal cortex. Toward this end, we will first provide an updated overview of the functional anatomy of macaque temporo-parieto-frontal connectivity, based on data collected mostly in the last decade, showing that these connections are an ensemble of different streams linking specific temporal, parietal, and frontal areas and taking part in large-scale, functionally specialized networks for controlling different aspects of behavior. Then, based on anatomical and functional evidence from human studies, we will consider possible homologies with the corresponding connectivity of the human brain to suggest that in primate evolution, phylogenetically old neural pathways and mechanisms have been retained and, in the human lineage, have been exploited for the emergence of human-specific cognitive capabilities.

2. The macaque posterior parietal cortex (PPC)

The macaque posterior parietal cortex (PPC) is a large cortical region that, as in the human brain, is subdivided by the intraparietal sulcus (IP) into a superior (SPL) and inferior (IPL) parietal lobule. As a whole, the PPC is primarily dedicated to the analysis of diverse, high-order aspects of sensory information, with special emphasis on visual information. One main aim of this type of processing is to use sensory information for the guidance of motor behavior, based on the integration of sensory and motor signals mediated by strong and reciprocal connections with the motor (primary motor and premotor) cortex (see, e.g., Caminiti et al., 2015; Rizzolatti, Luppino, & Matelli, 1998). This integration is the basis of so-called “sensorimotor transformations,” a neural mechanism in which automatically processed sensory information leads to the activation, in the motor cortex, of representations of “potential actions” (see, e.g., Cisek & Kalaska, 2010; Cisek, 2007; Rizzolatti & Luppino, 2001).

For a long time, it was believed that the SPL was exclusively dedicated to the analysis of higher-order aspects of somatosensory information originating from the primary somatosensory cortex, which is located in the postcentral gyrus. In contrast, the IPL was believed to be the main target of the occipito-parietal visual information processing pathway, usually referred to as the “dorsal visual stream,” which is primarily involved in space processing (Ungerleider & Mishkin, 1982). Non-human primate research over the last two decades has led to a radically different view of the

organization of the PPC, involving the following major aspects (for reviews, see, e.g., Caminiti et al., 2015; Colby, 1998; Rizzolatti et al., 1998; Rizzolatti, Fogassi, & Gallese, 1997). First, the PPC is formed by a multiplicity of distinct sensorimotor areas (Figure 1), located in both the SPL and the IPL, which are involved in the analysis of specific aspects of sensory information and are related to the control of specific effectors. Second, a majority of these areas are involved in the analysis of visual information, alone or in combination with somatosensory information. Third, visually related PPC areas, fed by the dorsal visual stream, are located not only in the IPL but also in the SPL. Finally, PPC areas of the IPL display robust, topographically organized connections with areas of the temporal cortex.

3. Parieto-frontal connectivity and general subdivision of the PPC

Anatomical studies have shown that almost the entire extent of the PPC is linked by strong and reciprocal connections to the motor cortex. Specifically, from early connectional studies of parieto-frontal connectivity (e.g., Pandya & Kuypers, 1969; Petrides & Pandya, 1984), it has become clear that these connections are topographically organized, with the SPL and IPL being mostly connected with more dorsal (PMd) and more ventral (PMv) parts of the premotor cortex. In later studies, the issue of the topographic organization of parieto-frontal connectivity was re-addressed in light of data showing that both the PPC and the motor cortex are formed by several anatomically and functionally independent areas (see, e.g., Rizzolatti & Luppino, 2001; Rizzolatti et al., 1998).

One major general finding of these studies was that parieto-frontal connections are organized in a rather specific way, and that each parietal area appears to have a privileged target in the frontal cortex. Based on these privileged connections, it is thus possible to identify a series of largely segregated parieto-frontal circuits linking specific PPC areas with specific motor areas. Functional evidence indicates that parietal and frontal areas forming a given circuit tend to have similar functional properties and appear to be jointly involved in specific aspects of sensorimotor transformations, based on the full integration of sensory and motor signals, at both the parietal and frontal level. Accordingly, this anatomical organization of parieto-frontal connections represents the substrate for a parallel processing of different aspects of sensorimotor transformations. It has been proposed that these parieto-frontal circuits represent the functional units of the cortical motor system (Rizzolatti et al., 1998).

Based on their general functional properties and patterns of frontal connectivity, the various PPC areas can be grouped into a rostral and a caudal domain, in both the SPL and the IPL. In the SPL, a more rostral domain includes two mostly somatomotor areas, PE and PEa. One major feature of the

neural activity in these areas is the integration of multi-joint sensory and motor signals related to arm/hand position and movement direction, which can be used for encoding egocentric representations of reaching, which are essential for guiding arm movements in space (e.g., Lacquaniti & Caminiti, 1998; Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995). Frontal connections of these areas (Figure 2A) involve the primary motor area F1 and the rostrally adjacent corticospinal areas F2 and F3 (SMA) located in the PMd and medial premotor cortex, respectively (Bakola, Passarelli, Gamberini, Fattori, & Galletti, 2013; Caminiti, Zeger, Johnson, Urbano, & Georgopoulos, 1985; Marconi et al., 2001; Matelli, Govoni, Galletti, Kutz, & Luppino, 1998; Tanné-Gariépy, Rouiller, & Boussaoud, 2002).

A more caudal SPL domain consists of a group of several visuomotor areas, such as V6A, PGm, PEc, and MIP, which are differentially connected (Figure 2B) with the PMd areas F7 and F2 (Bakola, Gamberini, Passarelli, Fattori, & Galletti, 2010; Gamberini et al., 2009; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Johnson, Ferraina, & Caminiti, 1993; Marconi et al., 2001; Matelli et al., 1998; Tanné-Gariépy et al., 2002). Two of these areas—V6A and PGm—are also connected to the dorsal part of prefrontal area 46 (46d; Gamberini et al., 2009; Leichnetz, 2001; Saleem, Miller, & Price, 2014), a region originally considered to be involved in encoding visuospatial information in working memory (see, e.g., Levy & Goldman-Rakic, 2000). These caudal SPL areas, in general, combine visuospatial information with gaze- and arm-related signals for visuomotor control of arm-reaching movements (for reviews, see, e.g., Caminiti et al., 2015; Fattori, Breveglieri, Bosco, Gamberini, & Galletti, 2015). Visual information sent to these areas mostly originates from the extrastriate motion-sensitive area V6 (Galletti et al., 2001), where the representation of the visual periphery is relatively emphasized (Galletti, Fattori, Battaglini, Shipp, & Zeki, 1996). Altogether, these data have supported the notion that caudal SPL–PMd connectivity is primarily involved in visuomotor control of reaching behavior. The finding that reaching neurons in area V6A can also be modulated by grasping movements has suggested its broader role in visuomotor control of reaching-to-grasp actions. Parieto-frontal connectivity of the areas of both the rostral and caudal SPL domains is supported by the first branch of the superior longitudinal fasciculus (SLF I; Schmahmann et al., 2007).

In the IPL, a more rostral domain includes the somato- and visuo-motor areas PF, PFG, and AIP, which are devoted to the control of goal-directed hand and mouth actions. These areas are tightly connected (Figure 2C) to the various subdivisions of the PMv area F5 (F5p, F5c, and F5a/44) and to the ventrolateral prefrontal (VLPF) areas ventral 46 (46v) and 12r (Borra et al., 2008; Cavada & Goldman-Rakic, 1989b; Petrides & Pandya, 1984; Rozzi et al., 2006). Specifically, areas AIP and PFG are two hand-related areas and are targets of dorsal visual stream information originating from

the motion-sensitive area MST and the caudal intraparietal (CIP) area, in which neurons code 3D objects' visual features (Sakata, Tsutsui, & Taira, 2005). AIP and PFG, together with F5, play a crucial role in selecting and organizing object-oriented hand actions (for a review, see Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014). Specifically, different lines of evidence have clearly shown that AIP and F5 are jointly involved in visuomotor transformations for grasping; that is, the selection of appropriate patterns of distal hand configurations based on visual coding of an object's physical properties. Furthermore, PFG and F5 appear to be jointly involved in selecting hand actions according to the goal or motor intention, reflecting sequential action organization. Finally, areas PFG and AIP, as well as F5, host visuomotor hand-related "mirror" neurons that activate during action observation (Fogassi et al., 2005; Maeda, Ishida, Nakajima, Inase, & Murata, 2015; Rizzolatti et al., 2014) and represent the parietal node of the so-called "mirror system," in which observed actions are mapped onto the corresponding motor representations and which is deemed to be the basis of action and intention understanding (Rizzolatti & Craighero, 2004). A further IPL area that could be included within this domain is area LIP, located more caudally in the IP. Indeed, area LIP is an oculomotor area, selectively connected (Figure 2C) with the frontal eye field (FEF) and the adjacent oculomotor caudal prefrontal areas 45B, 8r, and caudal 46 (Andersen, Asanuma, Essick, & Siegel, 1990; Blatt, Andersen, & Stoner, 1990; Cavada & Goldman-Rakic, 1989b), which plays a crucial role in visuomotor transformations for controlling oculomotor behavior (e.g., Blatt et al., 1990). The connectivity of these more rostral IPL (including LIP) areas with PMv, prearcuate oculomotor, and VLPF areas appears to be supported mostly by the third branch of the superior longitudinal fasciculus (SLF III; Schmahmann et al., 2007).

Finally, a more caudal domain in the IPL includes two areas, PG and Opt, which are targets of strong projections from the motion-sensitive area MST (Rozzi et al., 2006) and correspond to the cortical sector originally defined as area 7a by Vogt and Vogt (1919). Differently from most other PPC areas, PG and Opt, through the second branch of the superior longitudinal fasciculus (SLF II; Schmahmann et al., 2007), display relatively widespread frontal connectivity (Figure 2D), as they are connected to different parts of both PMd and PMv and 46d and 46v and are strongly and reciprocally connected to rostral IPL and caudal SPL visuomotor areas (Cavada & Goldman-Rakic, 1989a, 1989b; Petrides & Pandya, 1984; Rozzi et al., 2006). Neurons in this parietal sector have large visual receptive fields, modulated by the orbital position of the eye or by the position of the head, and respond to different patterns of optic flow stimuli (Merchant, Battaglia-Mayer, & Georgopoulos, 2001). Most neurons also display movement-related activity, mostly related to arm-reaching in the rostral area PG and to saccades in the caudal area Opt (Battaglia-Mayer, Mascaró, Brunamonti, & Caminiti, 2005; Hyvärinen, 1981; MacKay, 1992; Mountcastle, Lynch,

Georgopoulos, Sakata, & Acuna, 1975). However, there are also neurons encoding both eye- and arm-directional visuomotor signals related to the contralateral space (Battaglia-Mayer et al., 2005), suggesting a role of this sector in representing action space for intended eye and/or arm movements toward the contralateral space. Furthermore, this sector hosts neurons that encode the location of the most salient stimulus and are involved in redirecting attention to stimuli appearing at novel, unattended locations (Constantinidis & Steinmetz, 2001a, 2001b, 2005; Mountcastle, Andersen, & Motter, 1981). Finally, visually responsive neurons that appear to support an object-referenced representation of space also appear in this sector (Chafee, Averbeck, & Crowe, 2007) and can be modulated by world-referenced information (Snyder, Grieve, Brotchie, & Andersen, 1998). Altogether, these data suggest that this caudal IPL sector, based on multisensory integration, contributes to the construction of representations of surrounding space and to spatial attentional processes for guiding the motor behavior of arms and/or eyes.

The notion that the PPC, or most of it, is primarily involved in sensorimotor (mostly visuomotor) transformations was formalized in the 1990s by Milner and Goodale (Milner & Goodale, 1993, 1995), who proposed that the dorsal visual stream could actually be considered, as a whole, a “vision for action” pathway. In this view, visuomotor transformations are mostly meant as fast, automatic, and unconscious processes carried out independently from perceptual processes, which are considered the exclusive province of the occipito-temporal “ventral visual stream,” leaving open the question of how and where perceptual and cognitive process modulate or steer voluntary motor behavior.

A different model of the general organization of visual information processing in the macaque PPC was subsequently proposed by Rizzolatti and Matelli (2003). According to this model, the various parieto-frontal circuits, fed by the dorsal visual stream, can be grouped into two anatomically and functionally distinct main components: the dorso-dorsal stream, formed by circuits linking SPL with PMd areas; and the ventro-dorsal stream, formed by circuits linking IPL with PMv areas and the FEF. This proposal was mostly founded on two sets of connectional data. First, caudal SPL and IPL visuomotor areas are targets of dorsal visual stream information originating mostly from different extrastriate visual areas—that is, areas V6 and MT/MST, respectively. Second, as noted since earlier tract-tracing studies (e.g., Seltzer & Pandya, 1984, 1994), the IPL, but not the SPL, is robustly connected with the temporal cortex. More recent studies focused on the cortical connectivity of the various visuomotor parietal areas have described in detail the organization of temporo-parietal connectivity, providing new insights into their potential contribution to motor and cognitive motor function.

4. The macaque temporal cortex

1 The macaque temporal cortex can be anatomically subdivided by the superior temporal sulcus
2 (STS) into an inferior and superior temporal gyrus and functionally subdivided into four main
3 domains: a purely visual domain, located in the inferior temporal gyrus (inferotemporal cortex, IT);
4 a multisensory domain, located along the upper bank of the STS; an auditory domain, located in the
5 superior temporal gyrus (STG) and the planum temporale; and a memory-related domain, located in
6 the medial temporal cortex.
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8 The first domain—the IT cortex—includes areas, located at different rostrocaudal levels, which
9 represent the progression in the temporal lobe of the ventral visual stream: the occipito-temporal
10 visual information processing pathways devoted to the analysis of object qualities and identities
11 (Ungerleider & Mishkin, 1982). This pathway comprises a set of bidirectional projections that, from
12 visual areas of the occipital cortex, run in a rostrocaudal direction to the temporal pole through the
13 IT areas TEO and TE (see, e.g., Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). This
14 connectivity is supported by the inferior longitudinal fasciculus (ILF; Schmahmann et al., 2007).
15 Visual information processing along this pathway was originally viewed as a serially and
16 hierarchically organized sequence of processing stages in which simpler features are aggregated to
17 obtain more complex object representations (see, e.g., Kravitz et al., 2013). This view has been
18 challenged by more recent data showing that the ventral visual stream is actually a complex
19 recurrent network supporting the parallel processing of different features used to build up
20 representations of what could be better defined as Real World Entities (RWEs)—that is, objects,
21 plants, animals, and conspecifics (see Orban, Zhu, & Vanduffel, 2014). Specifically, it is possible to
22 identify three parallel substreams running in the ventral bank of the STS (TEa/m) and dorsal and
23 ventral parts of TE that are preferentially involved in the analysis of 3D shape, 2D shape, and
24 material properties, respectively. These substreams converge in the rostral part of the IT, where
25 representations of known RWEs are generated.
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27 Connections of the IT cortex involve both temporal and extratemporal areas (Figure 3A).
28 Specifically, rostral IT areas display connections with the perirhinal cortex in the MTL, which can
29 be used for encoding visual information related to RWEs in long-term memory (see Yoshida, Naya,
30 & Miyashita, 2003) and with the upper bank of the STS (Saleem, Suzuki, Tanaka, & Hashikawa,
31 2000). Extratemporal connections involve the frontal and parietal cortex (Saleem, Kondo, & Price,
32 2008; Seltzer & Pandya, 1989, 1994; Webster, Bachevalier, & Ungerleider, 1994) and run through
33 the extreme capsule/uncinate fasciculus and the ILF, respectively (Schmahmann et al., 2007). In the
34 frontal cortex, IT connections involve orbitofrontal areas 11, 13, and 12o, where visual information
35 can be used for the computation of good identities and subjective values in an abstract
36

representation (see, e.g., Padoa-Schioppa & Cai, 2011). Furthermore, IT areas display robust connections (Gerbella, Belmalih, Borra, Rozzi, & Luppino, 2010; Saleem et al., 2014; Schall, Morel, King, & Bullier, 1995; Stanton, Bruce, & Goldberg, 1995) with caudal prefrontal oculomotor areas (FEF, 45B) and, especially for area TEa/m, with VLPF areas—mostly area 12r—originally considered to be involved in working memory for objects and shapes (Wilson, Scalaidhe, & Goldman-Rakic, 1993) and in conditional learning based on object identity (Passingham, Toni, & Rushworth, 2000). This last connection is generally viewed as the progression in the frontal lobe of the ventral visual stream (Kravitz et al., 2013). Finally, the IT cortex, especially area TEa/m of the lower bank of the STS, is also robustly connected with the IPL, much more to the two intraparietal areas, the oculomotor area LIP, and the hand-related area AIP; and much less to IPL convexity visuomotor areas, except for the caudal-most area Opt (Borra et al., 2008; Cavada & Goldman-Rakic, 1989b; Rozzi et al., 2006; Seltzer & Pandya, 1994; Webster et al., 1994).

The second domain corresponds to a relatively large cortical sector, including the rostral two-thirds of the upper bank of the STS, and is commonly referred to as the superior temporal polysensory area (STP; Bruce, Desimone, & Gross, 1981). Area STP is a site of convergence for visual information originating from both more caudal motion-sensitive and inferotemporal areas, auditory information originating from dorsally adjacent auditory areas of the STG, and somatosensory information likely originating from IPL areas (for reviews, see Cusick, 1997; Felleman & Van Essen, 1991). Indeed, most STP neurons are visually responsive, but over half of them also exhibit somatosensory and/or auditory responses (Bruce et al., 1981). It has thus been suggested that this area plays a role in the integration of information within and across modalities, subserving orienting behavior to novel stimuli (Baylis, Rolls, & Leonard, 1987; Bruce et al., 1981). Visually responsive neurons may have complex functional properties and have been extensively studied by Perrett and colleagues (for a review, see, e.g., Carey, Perrett, & Oram, 1997). In particular, STP visual neurons respond to various forms of biological motion, including the direction of gaze and head, mouth, or hand movements; they can also differentiate between self-produced actions and actions made by others, and they appear to code the intentionality of actions as well (Jellema, Baker, Wicker, & Perrett, 2000; Jellema & Perrett, 2003). Altogether, these data suggest a key role of this temporal sector in social cognition. More recent functional imaging and electrophysiological data have shown that biological motion processing involves areas of both the upper and lower bank of the STS. Specifically, the upper bank appears to be more sensitive to motion patterns—that is, to kinematic aspects of the actions—whereas the lower bank appears to be more sensitive to configuration changes—that is, the deformation of body shapes (Jastorff, Popivanov, Vogels, Vanduffel, & Orban, 2012; Orban, Zhu, & Vanduffel, 2014).

Intratemporal connections of area STP, in addition to the IT cortex (Saleem et al., 2000) and the STG (Seltzer & Pandya, 1978), involve the MTL (Insausti & Amaral, 2008). Extratemporal connectivity (Figure 3B) involves both the frontal cortex and the IPL, with a distribution mostly complementary to that of the IT cortex (Seltzer & Pandya, 1989, 1994). In the frontal lobe, area STP, mostly the rostral part, is connected to the medial prefrontal and orbitofrontal areas of the so-called “medial prefrontal network” (Saleem et al., 2008) and to the rostral part of the VLPF areas 12r and 46v. Furthermore, there are strong connections between nearly the entire extent of the STP and dorsal prearcuate oculomotor areas, rostral dorsolateral prefrontal areas, and caudal VLPF area 45A. These frontal connections run mostly through the EC. In the IPL, connections running into the middle longitudinal fasciculus (MdLF; Schmahmann et al., 2007) link the STP mostly with visuomotor areas PFG, PG, and Opt of the convexity cortex (Cavada & Goldman-Rakic, 1989a; Rozzi et al., 2006).

The third, more dorsal, domain corresponds to the auditory cortex, defined as the cortical region receiving significant thalamic input from one or more divisions of the medial geniculate complex (Hackett, 2011). It is well known that this domain displays a complex anatomical and functional organization and consists of several distinct areas (for reviews, see Hackett, 2011; Kaas & Hackett, 2000). Based on common anatomical and functional features, these areas are usually grouped into three regions. The primary areas are located in the planum temporale and are grouped into a centrally located “core” region, whereas the secondary areas are assigned to “belt” or “parabelt” regions, which are located around the core and extend into the STG. Auditory information from the core region progresses serially across regions along the medio-lateral axis, i.e., from core to belt, to the parabelt. Furthermore, the rostral parabelt (RPB) largely connects with the rostral belt areas, whereas the caudal parabelt (CPB) largely connects with the caudal belt areas. The rostrocaudal topography of the connections of the auditory areas represents the substrate for a rostrocaudal functional specialization of the parabelt region. Specifically, there is evidence that neurons located more rostrally in the auditory cortex are preferentially tuned for the type of auditory stimuli, whereas neurons located more caudally are preferentially tuned for the spatial localization of auditory stimuli. These data represent the functional basis for the organization of auditory information processing into “what” and “where” streams analogous to the cortical visual system.

Intratemporal projections from auditory areas are directed medially, toward the insular and retroinsular cortex; laterally, toward the STP; caudally, toward the caudal temporal area Tpt; and rostrally, ultimately targeting the MTL (Hackett, 2011; Muñoz-López, Insausti, Mohedano-Moriano, Mishkin, & Saunders, 2015). Extratemporal projections from the auditory cortex (Figure 3C) originate from the belt and parabelt areas and, through the EC, mostly target the prefrontal

cortex (Romanski et al., 1999). Specifically, the rostral parabelt is mostly connected to orbitofrontal areas 11 and 12o, to the frontal pole (area 10), and to VLPF areas 45A and 12l. In contrast, the caudal parabelt is mostly connected to dorsal prearcuate oculomotor areas, rostral area 46d, and area 45A. There are few if any projections from the belt and parabelt areas to the PPC. However, the auditory-related area Tpt, located just caudal to the belt, displays relatively robust projections to the IPL that appear to selectively involve area PG (Rozzi et al., 2006).

The fourth domain is represented by a set of areas located in the MTL, associated with the limbic system, which play a key role in the formation and consolidation of conscious or declarative memories based on convergent projections from sensory, polymodal, and reward-related cortical areas. Recent functional data have shown that sectors of the parahippocampal cortex are preferentially active for images of scenes (Kornblith, Cheng, Ohayon, & Tsao, 2013). It has been proposed that these sectors are involved in a distinct multisynaptic visual information processing pathway, stemming from area V4v and ultimately targeting the hippocampus and the temporal pole, which could play an important role in spatial memory and navigation (see Kravitz, Saleem, Baker, & Mishkin, 2011). The parahippocampal cortex is also a target of projections from the posterior cingulate cortex and from the IPL area Opt (Cavada & Goldman-Rakic, 1989a; Rozzi et al., 2006), suggesting a contribution of visuospatial dorsal visual stream information to this function.

5. Temporo-parietal connections and large-scale cortical networks for motor and cognitive motor functions

Data so far reviewed show that there is robust connectivity in the macaque brain between the PPC and the temporal lobe that almost exclusively involves the IPL. Furthermore, studies aiming to describe the cortical connectivity of individual anatomically and functionally characterized IPL areas (Cavada & Goldman-Rakic, 1989a; Blatt et al., 1990; Rozzi et al., 2006; Borra et al., 2008) have provided clear evidence for a topographic organization of IPL–temporal connectivity (Figure 4). Specifically, the two main intraparietal areas, AIP and LIP, are preferentially connected with areas of the IT cortex, mostly area TEa/m of the lower bank of the STS; whereas visuomotor IPL convexity areas PFG, PG, and Opt are preferentially connected with the multisensory area STP. Furthermore, area PG is also a target of the auditory-related area Tpt.

Altogether, these data have strongly contributed to further supporting the notion of a dual-stream organization of visuomotor processing in the macaque PPC, in which SPL and IPL areas take part in a dorso-dorsal and ventro-dorsal stream, respectively. In this context, the dorso-dorsal stream is a relatively “short” visuomotor pathway that, in a few steps from the visual extrastriate area V6

1 through the caudal SPL, conveys visual information with an emphasis on the visual periphery to
2 arm-related fields of the PMd. In this pathway, visual information is integrated with gaze and arm-
3 related somatosensory and motor signals for relatively fast feed-forward guidance and online
4 monitoring of reach-to-grasp actions (Fattori et al., 2015). In contrast, the macaque IPL is a region
5 where both dorsal and ventral visual stream information and higher-order multisensory information
6 from the STP is integrated with information on motor programs. This type of integration could
7 provide the neural substrate for the role of the ventro-dorsal stream in what could be defined as a
8 “perception-based” control of motor behavior (Rizzolatti & Matelli, 2003; see also Fogassi &
9 Luppino, 2005). The rostral IPL domain appears to be involved in motor and cognitive motor
10 functions related to the selection and organization of hand and mouth actions (in AIP and PFG) and
11 to oculomotor control (in LIP) and in action and intention understanding. The caudal IPL domain
12 appears to be involved in multisensory integration for the construction of representations of
13 surrounding space for guiding arm and eye motor behavior.
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24 In this context, the hand-related area AIP is extensively connected to several inferotemporal
25 areas, including strong connections to a specific sector of area TEa/m, located in its intermediate
26 part (Borra et al., 2008). Functional imaging and electrophysiological studies have provided clear
27 evidence for a role of this inferotemporal sector in 3D-shape coding and perception (Janssen,
28 Vogels, Liu, & Orban, 2001; Uka, Tanaka, Yoshiyama, Kato, & Fujita, 2000) and visual coding of
29 hand-object interactions (Barraclough, Keith, Xiao, Oram, & Perrett, 2009; Nelissen et al., 2011;
30 Perrett et al., 1989). The connections between the AIP and intermediate area TEa/m provide the
31 substrate for the potential interaction and exchange of visual and motor signals between these two
32 areas. Indeed, there is evidence for the synchronization of neural activity in the intermediate TEa/m
33 and AIP during 3D-shape discrimination (Verhoef, Vogels, & Janssen, 2011) as well as for the
34 contribution of AIP neurons to 3D-shape perception (Verhoef, Vogels, & Janssen, 2015). Thus, it is
35 possible that ventral visual stream information about object identity is broadcast from
36 inferotemporal areas directly to the AIP. Accordingly, visuomotor transformations for grasping,
37 carried out by the AIP-F5 parieto-frontal circuit, would rely on information related not only to the
38 visual coding of an object’s physical properties, i.e., “how” an object is made, but also to “what” the
39 object target of the action is. The connectivity between the AIP and inferotemporal cortex also
40 provides a direct link between components of the hand motor system and areas responsible for
41 object recognition—that is, an access of signals related to motor and haptic representations of hand
42 actions to the representations of object identity. Accordingly, these connections could play a crucial
43 role in the neural mechanisms underlying tactile object recognition.
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Differently from the AIP, the temporal connections of area PFG mostly involve sectors of the upper bank of the STS, corresponding to area STP. As mentioned in Section 4, this area 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). This area was originally considered the major source of visual action information to the parieto-frontal mirror system (Rizzolatti & Craighero, 2004). However, functional imaging data in conscious macaques determined that the observation of object-oriented actions activates cortical sectors located in both area STP and TEa/m (Nelissen et al., 2011). Correlations with connectional data showed that one activated sector of area TEa/m corresponded to the intermediate sector of this area connected to the AIP, whereas an activated sector of area STP corresponded to a sector of this area connected to area PFG. These data suggest that visual action information, encoded in the STS, is forwarded to parietal areas of the mirror system along two distinct functional routes. One route, from the TEa/m to AIP area, could provide visual descriptions of the type and immediate goal of hand actions made by others; the other route, from the STP to PFG area, could be involved in extracting the intention behind the observed motor act (Nelissen et al., 2011).

Recent connectional evidence in macaques has pointed out that the functional role of these temporo-parietal connections must be considered in the framework of a large-scale, functionally specialized cortical network. Indeed, connectional studies of VLPF areas have shown that a specific sector of area 12r, located in its intermediate part, is connected to area AIP, the anterior sector of area F5 (F5a), and the intermediate sector of area TEa/m, which, in turn, is connected to area AIP (Borra, Gerbella, Rozzi, & Luppino, 2011). These data suggest that these areas altogether are involved in a large-scale cortical network that provides the potential neural substrate for generating purposeful hand actions (Figure 5A). This network has been designated a “lateral grasping network” (Borra, Gerbella, Rozzi, Tonelli, & Luppino, 2014). In this context, area 12r, together with the adjacent interconnected area 46v, could represent the specific substrate for interfacing perceptual, cognitive, and sensorimotor hand-related processes. Specifically, area 12r is a possible substrate for the integration of the ventral visual stream with sensorimotor hand-related information in the prefrontal cortex. These data, in addition to data on the temporal connectivity of area AIP, provide strong support for the idea that the properties of ventral stream processing may not have originally evolved to play a role in pure perception, but may instead reveal its earlier and more fundamental role in collecting information useful for action selection (Cisek & Kalaska, 2010).

Inferotemporal areas also project to the oculomotor intraparietal area LIP. These projections originate from sectors of the TEa/m and inferotemporal convexity cortex located more caudally than those connected to the AIP area (Cavada & Goldmann-Rakic, 1989a; Blatt et al., 1990; unpublished observations). Indeed, the LIP hosts neurons showing shape selectivity, encoding non-spatial attributes of the stimuli, and activating during the observation of 2D shapes, thus likely reflecting input from ventral visual stream areas (Serenio & Maunsell, 1998; Toth & Assad, 2002). As for the temporal connectivity of area AIP, the functional role of these connections should be considered in the framework of a large-scale cortical network (Figure 5B). Indeed, the ventral part of the FEF, where small amplitude saccades are represented (Bruce, Goldberg, Bushnell, & Stanton, 1985), and even more so the ventral prearcuate area 45B, both robustly connected to the LIP, are also robustly connected to those IT sectors that serve as sources of projections to the LIP (Gerbella et al., 2010; Nelissen et al., 2011). In this network, area 45B would represent a prefrontal site of integration of spatial and non-spatial visual information on RWEs used for guiding oculomotor behavior (Gerbella et al., 2010).

The two caudal IPL convexity areas PG and Opt are robustly connected to area STP. Furthermore, area PG is a target of projections from the auditory-related area Tpt. As noted in Section 3, since early electrophysiological observations, it has been proposed that area STP may be involved in multisensory integration subserving orienting behavior to novel stimuli (Baylis et al., 1987; Bruce et al., 1981). In accord with this view, Perrett and colleagues have proposed that STP neurons belong to a system that detects unexpected and hence behaviorally relevant sensory events (Hietanen & Perrett, 1993; Mistlin & Perrett, 1990). Indeed, lesions involving area STP produce impairment in orientation toward stimuli in the contralateral space (Luh, Butter, & Buchtel, 1986). Furthermore, gaze- and body-part-direction-sensitive neurons can contribute to spatial attentional processes that provide information about the intentions of others (see Carey et al., 1997). Accordingly, STP input, as well as auditory-spatial information from area Tpt, could substantially contribute to the role of caudal IPL areas PG and Opt in higher-order visuospatial processing. As noted above, both caudal IPL areas and area STP have relatively widespread cortical connectivity, which could provide the substrate for their participation in different cortical networks. In this context, there is evidence that prefrontal area 46d, which was originally considered to be involved in visuospatial processing, is connected to both area STP and PG/Opt (Borra, Gerbella, Giorgetti, Rozzi, & Luppino, 2014; Petrides & Pandya, 1999), thus suggesting that temporo-parietal connections between the caudal IPL and area STP are also part of a large-scale, functionally specialized cortical network involved in spatial and attentional processing (Figure 5C). Caudal IPL areas, especially area Opt, are also connected to parahippocampal areas (Cavada & Goldman-Rakic,

1989a; Rozzi et al., 2006) of the medial temporal lobe that are involved in a scene-processing visual pathway that ultimately targets the hippocampus. Specifically, it has been proposed that the caudal IPL is at the origin of a parieto-medial temporal pathway that, directly or indirectly through posterior cingulate areas, contributes to the complex spatial processing required for navigating through the environment (Kravitz et al., 2013).

6. Possible homologies between the macaque and human temporo-parieto-frontal connectivity

The possible homologies between the macaque and human PPC have been a matter of debate (Luppino, 2005). In humans, lesions involving the PPC produce a large variety of clinical syndromes, according to their localization in the SPL versus the IPL and in the right versus the left hemisphere. Specifically, lesions centered on the SPL, independently from the side of the lesion, can determine optic ataxia (Perenin & Vighetto, 1988; Ratcliff & Davies-Jones, 1972), which can basically be defined as a disorder of visually guided movements of the arms toward a target. In contrast, lesions of the IPL can determine deficits that vary according to the side of the lesion. Lesions of the right IPL, especially its lower part, can produce neglect (Perenin & Vighetto, 1988; Vallar & Perani, 1986), which mostly manifests as the inability of a patient to process and perceive stimuli on the contralateral side of the body or space. Lesions of the rostral part of the left IPL, in correspondence to the supramarginal gyrus (SMG), can cause ideomotor apraxia, a higher-order motor deficit manifesting as a failure to transform the internal representation of a gesture into the appropriate motor actions. This failure is the foundation for the inability to replicate the same gesture following a verbal command, imitate in the absence of an object, and distinguish well-performed from poorly performed movements (De Renzi & Faglioni, 1999; Heilman, Rothi, & Valenstein, 1982). Indeed, Jeannerod and Jacob (2005) have proposed that, in humans, the dorsal visual stream is not a unitary functional system. Whereas the SPL is mostly involved in visuomotor transformations, the IPL is involved in high-level visuomotor representations that contribute, in the right hemisphere, to the perception of spatial relationships; and in the left hemisphere, to the storage of complex representations of actions. This view was difficult to reconcile with the notion that the macaque PPC is part of a “vision for action” visual stream involved in automatic visuomotor processing. As reviewed above, more recent data on macaques have highlighted a dual organization of the dorsal visual stream in which a dorso-dorsal “vision for action” stream is mostly involved in fast feed-forward guidance and online monitoring of reach-to-grasp actions, and a ventro-dorsal stream is involved in “perception-based” motor control. These data, together with functional and

structural data from human studies, have provided converging evidence for a general homology between the macaque and human PPC.

Indeed, the human rostral IPL, as in macaques, is involved in the neural mechanisms for selecting and controlling goal-directed hand actions and in action and intention understanding (Caspers, Zilles, Laird, & Eickhoff, 2010; Grosbras, Beaton, & Eickhoff, 2012; Molenberghs, Sale, & Mattingley, 2012; Rizzolatti et al., 2014). Specifically, two rostral IPL sectors appear more specifically engaged during object grasping and manipulation, visuomotor transformations for grasping, and planning of sequential goal-directed hand actions. The first, located in the lateral bank of the IP, is considered the human homolog of the macaque AIP (hAIP; see, e.g., Davare, Kraskov, Rothwell, & Lemon, 2011; Grafton, 2010). The second, located in the rostral SMG, corresponds to an architectonic area—PFt—considered the putative homolog of the macaque area PF/PFG (Caspers et al., 2006, 2010). These same IPL areas also activate during observation of object-oriented actions (e.g., Caspers et al., 2010; Grosbras et al., 2012; Molenberghs et al., 2012) and are considered a parietal node of the human mirror system involved in coding goals and intentions of others' actions (see Rizzolatti et al., 2014).

As in macaques, a branch of the SLF (SLFIII) in humans connects the rostral intraparietal sulcus and the SMG with the ventral premotor cortex and the inferior frontal gyrus (Makris et al., 2005; Thiebaut de Schotten, Dell'Acqua, & Valabregue, 2012). Thus the frontal target/origin of the SLFIII includes areas involved in hand action control and action and intention understanding, which can be considered at least in part homologous to the macaque area F5 (Rizzolatti & Arbib, 1998; Rizzolatti et al., 2014). Indeed, dMRI evidence for a linkage between the PMv/area 44 and anterior intraparietal sulcus/SMG (Caspers et al., 2011; Ruschel et al., 2014; Schubotz, Anwander, Knösche, von Cramon, & Tittgemeyer, 2010), an increase in effective connectivity between the human AIP 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 the human AIP (Davare, Rothwell, & Lemon, 2010) strongly favors the existence of IPL-PMv circuits for the visuomotor control of hand actions homologous to those within the macaque brain.

The human rostral IPL also displays an extensive connectivity with the temporal lobe. This connectivity appears to be mostly supported by a fiber system identified as the posterior segment of the arcuate fasciculus (AF) or the SLF (SLFV), linking the posterior part of the superior (STG), middle (MTG), and inferior (ITG) temporal gyrus with the SMG (Catani, Jones, & Ffytche, 2005; Martino et al., 2013; Wu, Sun, Wang, Wang, & Wang, 2016). Recent dMRI evidence has shown that connectivity between the STG and SMG could also be supported by the middle longitudinal fasciculus (MdLF; Makris, Zhu, Papadimitriou, Mouradian, & Ng, 2016). Note that in all these

1 studies, connectivity of the anterior intraparietal sulcus with the temporal cortex was not explicitly
2 investigated.

3 Functional imaging studies in humans have provided clear evidence for a cortical sector located
4 in the posterior ITG and fusiform gyrus (the lateral occipital complex, or LOC) in which different
5 sites are specifically active during the visual processing of shapes, faces, and actions (e.g., Denys et
6 al., 2004; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995; see also, Orban et al., 2014).
7 Based on comparative fMRI observations, Denis et al. (2004) proposed that the LOC could be the
8 human homolog of the lower bank of the STS (area TEa/m) and the laterally adjacent IT convexity
9 cortex in macaques.
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11 Notably, in humans, visuomotor processing for selecting and controlling hand actions carried out
12 in the rostral IPL is influenced by processing taking place in ventral visual stream areas, mostly in
13 the LOC (Bracci & Peelen, 2013; Gallivan, Cant, Goodale, & Flanagan, 2014; Majdandžić et al.,
14 2007; Verhagen, Dijkerman, Grol, & Toni, 2008). Furthermore, there is evidence that visual and
15 haptic coding of objects activates both the hAIP (Grefkes, Weiss, Zilles, & Fink, 2002) and LOC
16 (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; James et al., 2002; Reed, Shoham, &
17 Halgren, 2004), suggesting the multimodal representation of objects in the human ventral visual
18 stream and interactions between the hAIP and LOC for tactile object recognition (Lacey, Tal,
19 Amedi, & Sathian, 2009; Tal & Amedi, 2009).
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21 Dorsal to the LOC and in proximity to the posterior part of the STS (pSTS) is a region that
22 activates for visual, auditory, and somatosensory stimulation, suggesting multisensory integration
23 and homologies with the STP area in macaques (Beauchamp, Yasar, Frye, & Ro, 2008).
24 Furthermore, the human STS, especially the caudal part, is responsive to diverse types of biological
25 motion and is considered a key node of the so-called “social brain” (Allison, Puce, & McCarthy,
26 2000; Frith & Frith, 2007). Biological motion processing in this region appears to concern mostly
27 kinematic aspects, whereas in the LOC it appears to concern mostly configuration changes of the
28 observed actions, further supporting the homology of this region with the STP in macaques and,
29 also as in macaques, suggesting a dual-stream processing of action observations (Jastorff, Kourtzi,
30 & Giese, 2009). These sectors of the posterior MTG/STS and LOC are considered the major source
31 of visual action information to the mirror system (Caspers et al., 2010; Grosbras et al., 2012;
32 Molenberghs et al., 2012; Rizzolatti et al., 2014). Combined, these data suggest that within the
33 general framework of the temporo-parietal connectivity of the human rostral IPL, there are
34 components equivalent to the macaque pathways connecting the TEa/m and AIP, and the STP and
35 PFG, respectively.
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1 However, in the left hemisphere, the SMG, posterior MTG/ITG, and PMv/area 44 are also
2 involved in cognitive abilities unique or almost unique to humans, such as higher-order aspects of
3 organizing object-oriented actions, including tool use (Johnson-Frey, Newman-Norlund, & Grafton,
4 2005; Peeters et al., 2009; Peeters, Rizzolatti, & Orban, 2013; Rilling et al., 2012) and imitation
5 (Buccino et al., 2004; Caspers et al., 2010; Rizzolatti et al., 2014). These cognitive abilities could
6 have emerged in primate evolution from the exploitation and adaptation of the phylogenetically
7 older neural mechanisms and pathways for hand action organization and action and intention
8 understanding that take place in the lateral grasping network of macaques, resulting in the
9 expansion and differentiation of the homologous regions and pathways of the human brain (Figure
10 6A; e.g., Hecht et al., 2013; Johnson-Frey et al., 2005; Johnson-Frey, 2004; Orban & Caruana,
11 2014; Ramayya, Glasser, & Rilling, 2010; Rizzolatti et al., 2014).

12 Specifically, based on dMRI observations, Hecht et al. (2013) suggested that a stronger and more
13 extensive connectivity of MTG regions involved in the visual coding of actions and ITG regions
14 involved in shape and action coding with the SMG, as well as stronger connectivity between the
15 SMG and PMv/area 44, differentiate the cortical mirror network of humans from macaques and
16 could have contributed to the emergence of the role of this system in imitation and imitation
17 learning (see also Rizzolatti et al., 2014). Furthermore, the differentiation of MTG areas responsible
18 for storing conceptual and semantic information about tools, and of a rostral SMG sector devoted to
19 tool use and their interconnectivity, could have contributed to the emergence of tool use based on
20 the exploitation of the phylogenetically older neural mechanisms that occur in the lateral grasping
21 network (Orban & Caruana, 2014; Peeters et al., 2009, 2013; Ramayya et al., 2010).

22 In the right hemisphere of human brains, a cortical region that includes the ventral part of the
23 angular gyrus (AG), the SMG, and the adjacent caudal temporal cortex (temporo-parietal junction,
24 TPJ) plays an important role in higher-order aspects of visuospatial and attentional processing
25 (Corbetta, Patel, & Shulman, 2008). Specifically, it has been proposed that in the human brain,
26 there are two main large-scale cortical networks involved in attending to environmental stimuli,
27 designated the dorsal and ventral attention network (Corbetta, Patel, & Shulman, 2008; see also
28 Bartolomeo, Schotten, & Chica, 2012; Corbetta & Shulman, 2011). The dorsal attention network
29 includes oculomotor and visuospatial processing areas of the medial IP, SPL, and frontal
30 oculomotor areas and would be more involved in spatial orienting. Considering that the human
31 homolog of the macaque LIP appears to be located in the medial IP (Grefkes & Fink, 2005; Orban,
32 2016), this network, to some extent, could represent the human equivalent of the oculomotor
33 parieto-frontal circuitry in macaques, linking area LIP to frontal oculomotor areas. The ventral
34 attention network includes the TPJ/IPL and ventral frontal cortex. This network could play a role in

detecting salient and behaviorally relevant stimuli in the environment, especially when unattended. These systems dynamically interact during normal perception to determine where and what to attend to. Connectional evidence from dMRI observations has shown that the parieto-frontal connectivity of the dorsal network is supported by the SLFI, whereas that of the ventral network is supported by the SLFIII and is more developed in the right hemisphere (Thiebaut de Schotten et al., 2011). Furthermore, the TPJ/IPL, through the SLFII, is also connected to the frontal components of the dorsal network. These connections of the human TPJ/IPL with both dorsal and ventral frontal areas closely resemble those of the caudal IPL in macaques (areas PG and Opt). Similar to the caudal IPL in macaques, which displays temporal connectivity with the auditory STG area Tpt, STP, and IT, the TPJ/IPL is also connected with the STG, MTG, and ITG through the posterior segment of the AF and the MdLF (Catani et al., 2005; Makris et al., 2016; Martino et al., 2013; Wu et al., 2016). In the right hemisphere, the STG/MTG, TPJ/IPL, and IFG/PMv are the most frequent anatomical correlates of spatial unilateral neglect (Corbetta & Shulman, 2011; Halligan, Fink, Marshall, & Vallar, 2003), and have been included by Karnath and Rorden (2012) in a so-called “cortical network for spatial neglect” (Figure 6B). Indeed, it has long been proposed that attentional spatial processes that may be disrupted in neglect do not result from the activity of single-brain areas but rather emerge from the interaction of large-scale networks (see, e.g., Bartolomeo, Thiebaut De Schotten, & Doricchi, 2007; Heilman, Bowers, Valenstein, & Watson, 1993; Mesulam, 1981). In this context, it has been suggested that the parietal component of the ventral attention network includes evolutionarily new areas, not present in macaques, which could be responsible of higher-order aspects of attentional control, including non-spatial attentional processes considered unique or almost unique to humans (Bartolomeo et al., 2012; Corbetta & Shulman, 2011; Patel et al., 2015). Altogether, these data favor topological and connectional homologies between the human TPJ/IPL and the macaque caudal IPL (areas PG and Opt) and suggest that higher-order supramodal attentional processing of the human right IPL, more detached from action, could have evolved from the exploitation and adaptation of the neural mechanisms underlying spatial processing for eye and/or arm movements that occur in caudal IPL areas in macaques.

7. Concluding remarks

The primary aim of this review was to describe the detailed organization of the temporo-parieto-frontal connectivity of the macaque brain, based on tract-tracing studies of the connectivity of individual anatomically and functionally defined areas. These studies show that such connections link specific temporal areas with specific IPL and ventral frontal areas, which are in turn

interconnected, thus providing the neural substrate for large-scale cortical networks for controlling higher-order aspects of motor behavior and cognitive motor functions, in which the various nodes are linked through “dorsal” temporo-parieto-frontal and “ventral” temporo-frontal pathways. This is the case, for example, in the large-scale cortical network for action organization and action and intention understanding involving the rostral IPL, as well as the large-scale cortical network for visuospatial and attentional processing involving the caudal IPL.

This organizational picture appears to have been conserved in primate evolution. Indeed, there is clear evidence for human equivalents of these networks (Caspers et al., 2010; Corbetta & Shulman, 2011; Grosbras et al., 2012; Karnath & Rorden, 2012; Molenberghs et al., 2012; Rizzolatti et al., 2014), including both “dorsal” and “ventral” pathways, in which the macaque neural mechanisms for action organization, action and intention understanding, and visuospatial and attentional processing have been conserved and exploited for the emergence of human-specific cognitive capabilities, such as tool use, imitation learning, and non-spatial attentional processes. Accordingly, fine-grained connectional data from macaque studies could be essential for understanding human brain mechanisms, even in cases of cognitive abilities not developed in other animals. Furthermore, these data could be helpful for the interpretation of clinical data, including disconnection syndromes, considering that even more modern dMRI approaches can fail in solving fiber crossings and following bundles within fiber tracts, thus preventing the identification of the specific components forming a given fiber tract.

In this context, some features of human temporo-parieto-frontal connectivity still need to be interpreted in light of the general homologies between the macaque and human brain. This is the case, for example, with the temporal connectivity of the SPL, for which there is evidence from both dMRI and fiber dissection observations, although it still lacks a univocal definition. Specifically, it has been reported (although with some differences across studies) that these connections involve, in the temporal cortex, 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, Sair, Radmanesh, & Hasan, 2014; Makris et al., 2009, 2013, 2016; Wang et al., 2013; Wu et al., 2016). These connections appear to run through either the MdLF (Kamali et al., 2014; Makris et al., 2009, 2013, 2016; Wang et al., 2013), a fiber system considered a component of the AF/SLF (Kamali et al., 2014), or an independent bundle (Wu et al., 2016). This connection 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, Jastorff, & Orban, 2013) or visuo-auditory attentional processing (Hecht et al., 2013; Wang et al., 2013; Makris et al., 2016). Furthermore, Hecht et al. (2013) described a connection

between the SPL and inferior frontal areas, not present in the macaque brain; however, this connection has not been observed in other studies. Yet, it should be noted that Brodmann's area 7 is a large, heterogeneous cortical region that includes not just sectors potentially homologous to the macaque visuomotor area V6A, PEc, and MIP, but also extends medially into the precuneus, which likely hosts sectors homologous to the macaque area PGm and posterior cingulate cortex (see, e.g., Pitzalis, Fattori, & Galletti, 2015); and laterally into the IP, which hosts the putative homolog of the macaque LIP (see, e.g., Orban, 2016). As mentioned in Section 4, in the macaque, area LIP and the posterior cingulate cortex are provided with connections to the IT and medial temporal areas, respectively. Accordingly, it is possible that the temporo–SPL connectivity described in the human brain at least in part includes equivalents of these connections in the macaque brain. Thus, it is possible that the temporal connections of the putative human homolog of the macaque LIP are part of a cortical network equivalent to the “oculomotor network” described in Section 5 (Figure 5B). Future studies are needed to better define the various, potentially phylogenetically older and newer components of human temporo–SPL connectivity.

Acknowledgements

The work from our laboratory has been supported by Ministero dell'Istruzione, dell'Università e della Ricerca (grant number: PRIN 2010, 2010MEFNF7_005) and by the European Commission Grant Cogsystems FP7-250013.

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Figure legends

Figure 1. Schematic view of the lateral, medial, and orbitofrontal cortical surface of the macaque brain showing the areal subdivision of the posterior parietal, temporal and frontal cortex. The superior (SA) and inferior (IA) arcuate, the intraparietal (IP) and the superior temporal (ST) sulci are shown unfolded to display the location of cortical areas buried in their banks. P, C, L, and Lu on the lateral view of the hemisphere indicate the principal, central, lateral, and lunate sulcus, respectively. Cg and PO on the medial view of the hemisphere indicate the cingulate and the parieto-occipital sulcus, respectively. LO and MO in the orbito-frontal cortex indicate the lateral and medial orbital sulcus, respectively. Parietal areas are defined according to architectonic criteria described by Pandya and Seltzer (1982), Luppino, Ben Hamed, Gamberini, Matelli and Galletti (2005), and Gregoriou, Borra, Matelli and Luppino (2006), except for the areas of the IP, defined according to functional and connectional criteria (see Colby, 1998; Rizzolatti et al., 1998). Temporal areas are defined according to architectonic and functional criteria according to Seltzer and Pandya (1978) and Boussaoud, Ungerleider and Desimone (1990) and Hackett, Stepniewska and Kaas (1998). Agranular frontal (motor) areas are defined according to architectonic criteria described by Matelli, Luppino and Rizzolatti (1991) and Belmalih et al. (2009). Prefrontal areas are defined according to architectonic criteria described by Carmichael and Price (1994) and Gerbella, Belmalih, Borra, Rozzi and Luppino (2007).

Figure 2. Summary view of the main frontal connections of the macaque PPC. A: Connections of rostral SPL areas. B: Connections of caudal SPL areas. C: Connections of rostral IPL areas. D: Connections of caudal IPL areas.

Figure 3. Summary view of the main frontal and parietal connections of the macaque temporal cortex. A: Connections of the ventral visual stream areas of the inferotemporal cortex. B: Connections of the multisensory area STP. C: Connections of the auditory parabelt areas of the superior temporal gyrus.

Figure 4. Summary view of the topography of the temporo-parietal connectivity of the macaque brain.

Figure 5. Examples of large-scale functionally specialized temporo-parieto-frontal networks, based on tract tracing connectional data in the macaque brain. A: Network for controlling hand actions. B: Network for controlling oculomotor behavior. C: Network for visuospatial and attentional processing.

Figure 6. Cortical sectors of the human brain involved in action observation and imitation (A) and most frequently correlated with spatial unilateral neglect (B) and their possible interconnections. Based on data from Casper et al. (2010), Rizzolatti & Sinigallia (2016), Corbetta & Shulman, 2011) and Karnath & Rorden (2012)

*Highlights

Robust connections link the macaque temporal and inferior parietal cortex

These connections are part of large-scale cortical networks involved in motor and cognitive motor functions

This organizational picture appears to have been conserved in primate evolution

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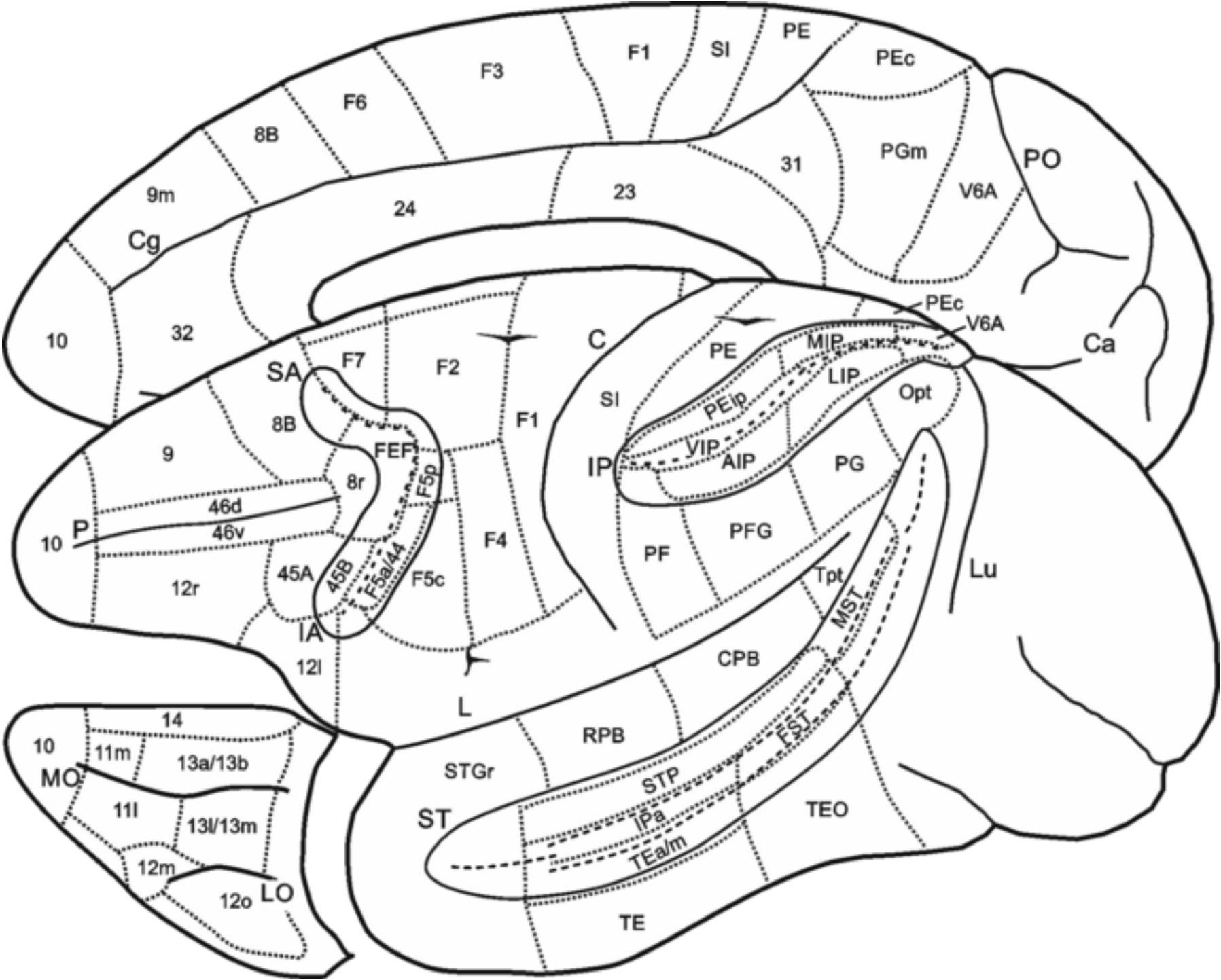


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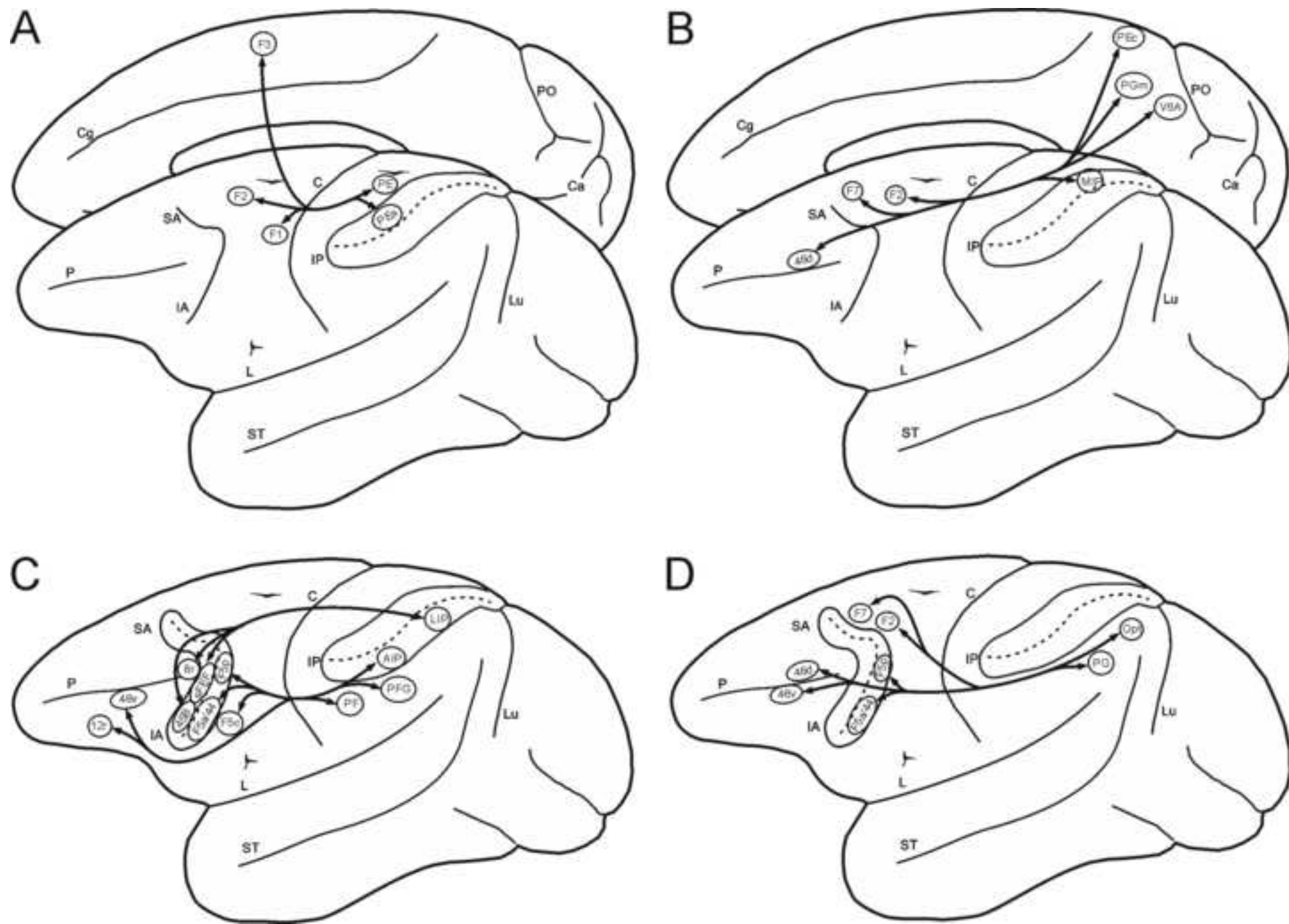


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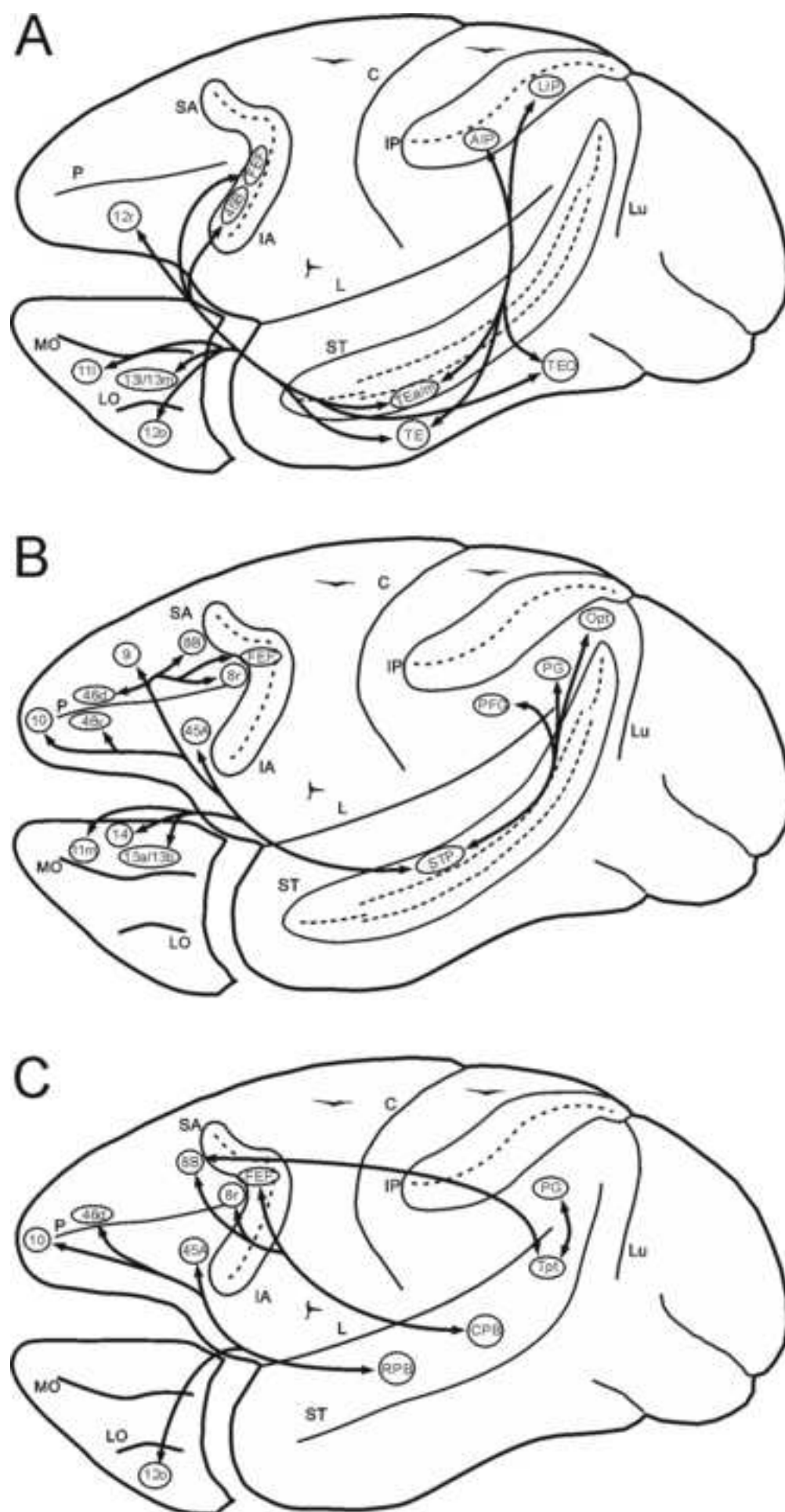
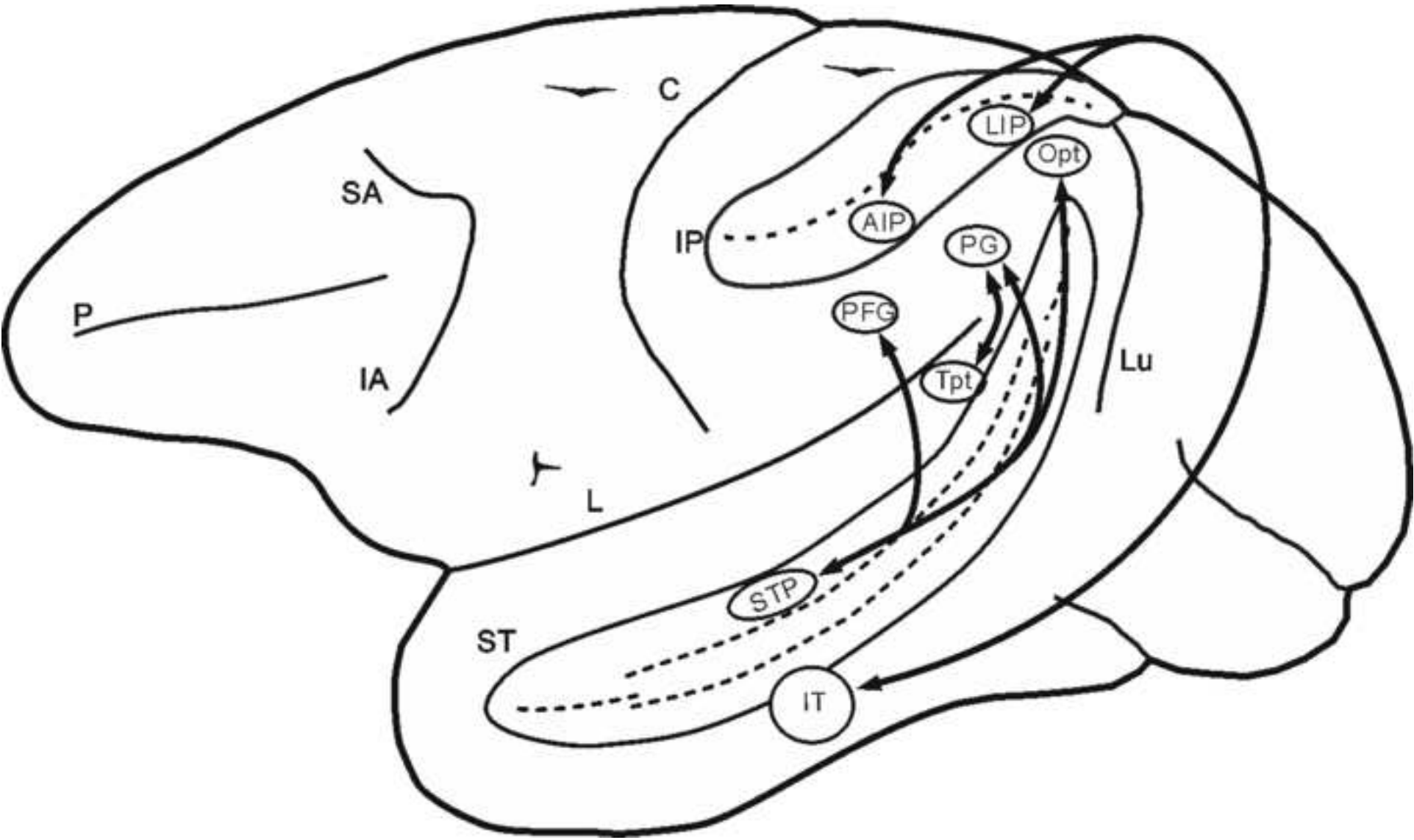
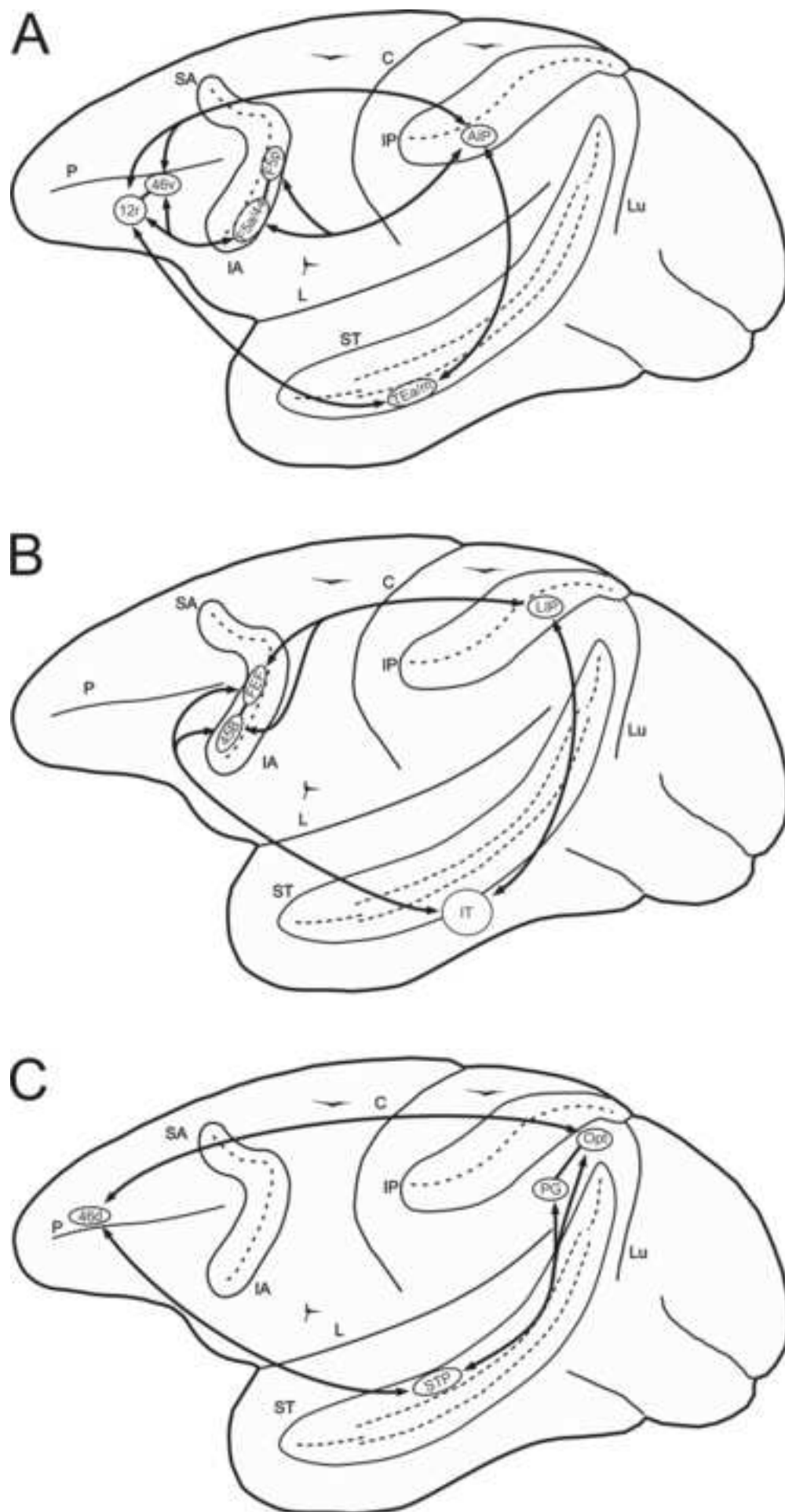


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