

a0005

Reaching and Grasping

S Budisavljevic and U Castiello, University of Padua, Padova, Italy

© 2017 Elsevier Inc. All rights reserved.

Introduction	1
Reaching	1
Reaching in the Monkey	1
Reaching in Humans	3
Neuropsychological Evidence	3
Neuroimaging and Transcranial Magnetic Stimulation	3
Grasping	4
Grasping in the Monkey	4
Grasping in Humans	5
Neuropsychological Evidence	5
Evidence From Neuroimaging and TMS	5
Further Reading	7

s0010

Introduction

p0010

According to a long standing idea, reaching movements are supported by the dorsomedial parietofrontal circuit consisting of the superior parietal lobule (SPL) and the dorsal premotor cortex (PMd), whereas grasping movements entail the dorsolateral parietofrontal network involving the inferior parietal lobule (IPL) and the ventral premotor cortex (PMv). Recently, however, this dichotomist organization has been put into question given that it does not mirror the anatomical and functional organization of reaching and grasping movements. It has been shown that the anatomical pathways linking the posterior parietal cortex to PMd and PMv partially overlap. Also SPL, PMd and PMv contain cells encoding reach direction as well as the orientation and shape of a target object, hand orientation and grip formation necessary for efficient grasping. Furthermore, both the dorsolateral and the dorsomedial networks are active during grasping in humans. Thus, the new evidence questions the existence of two separate circuits for reaching and grasping and suggests that they are likely to be involved in both actions.

s0015

Reaching

p0015

Reaching towards objects requires the solution of a complex spatial problem, given that different coordinate systems are involved in the coding of the position of the reaching hand and of the position of the target object. In order to perform a successful reaching movement towards an object, signals about limb starting position, eye position and target location all have to be combined and integrated into a common, distributed spatial representation. A central role for such integration, played by a neural circuit involving the frontal and the parietal cortex, has been revealed by neurophysiological, neuropsychological, and neuroimaging evidence. This circuit comprises motor areas and regions located in the frontal lobe as well as posterior parietal regions. The evidence emphasizes the role of the posterior parietal cortex in space perception and guiding actions, indicating that the sensory control of movement depends crucially on this region. The fundamental role ascribed to the posterior parietal cortex follows from its anatomical location. It is localized between the visual cortex behind it in the occipital lobe and the somatosensory cortex in front of it in the postcentral gyrus. This makes it well positioned to associate visual and somatosensory information, as well as to send output to premotor and motor areas in the frontal cortex, which is also fundamental for the control of reaching movements.

s0020

Reaching in the Monkey

p0020

By means of single-unit recording techniques, a number of studies have indicated the presence of frontal (PMd) and parietal reach-related neurons with the capacity to integrate different spatial variables relative to the structure of the external world, such as spatial location, distance, physical dimension, as well as perform some of the associated visuomotor transformations required for successful visually guided movements (Fig. 1A)).

☆Change History: October 2015. Sanja Budisavljevic and Umberto Castiello updated Abstract, Keywords and the Further Reading section, modified Figures 2 and 3 and added new Figures 4 and 5.

2 Reaching and Grasping

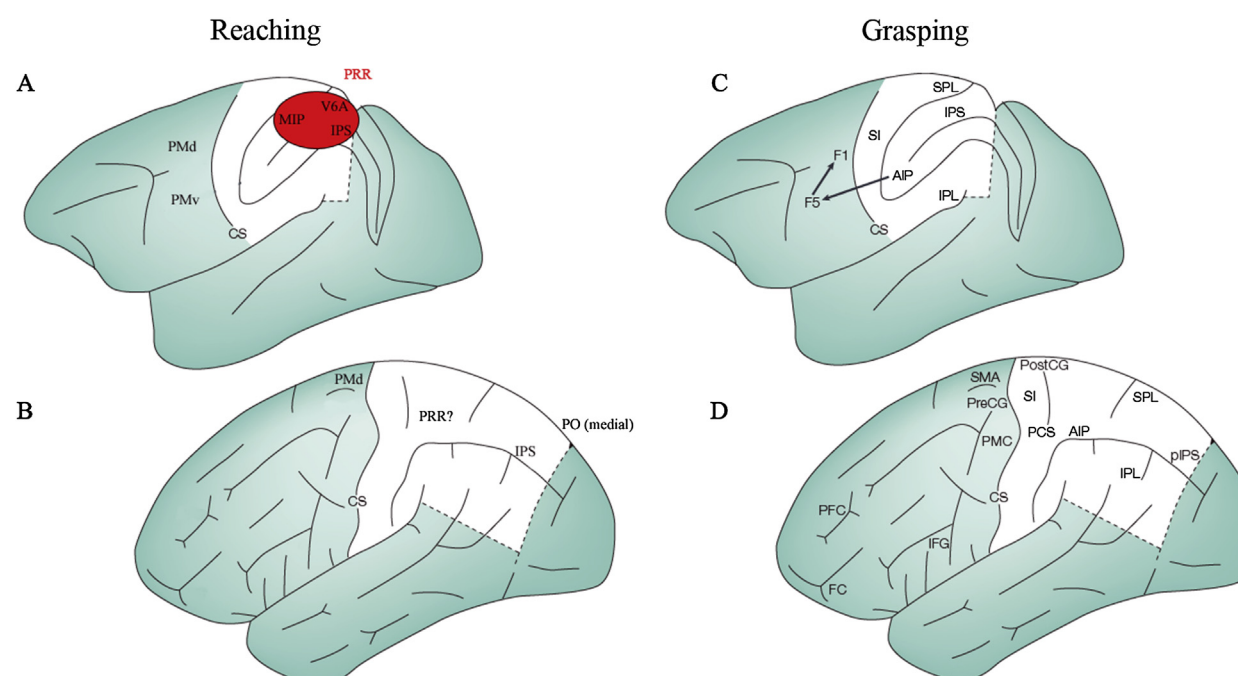


Figure 1 Comparison between neural circuits for reaching and grasping in the macaque monkey and humans. Lateral view of the monkey and human cerebral cortex for both reaching (panels A and B, respectively) and grasping (panels C and D, respectively) circuits. Panel “A” represents the parietal reach region for reaching as identified in monkeys. Panel “B” represents reaching areas in humans as identified by neuroimaging studies. Panel “C” represents the visuomotor stream for grasping as identified in monkeys. Panel “D” represents the grasping areas as identified in humans by neuroimaging studies. Cortical areas that control grasping are also connected with basal ganglia and cerebellar circuits. These circuits, although involved in grasping, are not shown in the figure. Abbreviations: *AIP*, anterior intraparietal area; *CS*, central sulcus; *IPL*, inferior parietal lobule; *MIP*, medial intraparietal area; *PCS*, postcentral sulcus; *PFC*, prefrontal cortex; *PreCG*, precentral gyrus; *PostCG*, postcentral gyrus; *PMC*, premotor cortex; *PMd*, dorsal premotor cortex; *PMv*, ventral premotor cortex; *PRR*, parietal reach region; *SI*, primary somatosensory cortex; *SMA*, Supplementary motor area; *SPL*, superior parietal lobule.

Studies conducted on macaque monkeys have shown that a number of sub-areas of the posterior parietal cortex, named collectively as the parietal reach region (PRR) (Fig. 1A), contain neurons that respond during the execution of reaching movements. For instance, activity within a visual area (area V6A) located in the SPL of the monkey, was found when the animal was instructed to push or pull a lever positioned outside the field of view. Furthermore, inactivating the PRR region at the level of the medial bank of the intraparietal sulcus (MIP, Fig. 1A), lead to increased errors for reaching movements to visual stimuli, but not for eye movements to the same stimuli. However, the errors were present only for targets shown in the peripheral but not in the central visual field (similar to deficits observed in the human optic ataxia patients, discussed below). These studies strongly support the notion that PRR is causally involved in reach-specific visuomotor pathways.

Another important finding suggested that eye-position signals influence reaching-related activity not only in the parietal areas but also in regions of the frontal cortex such as the dorsal and the ventral premotor cortex. The frontal areas contributed to the target localization in space and therefore to the transformation from visuospatial to motor coordinates necessary for successful reaching. In line with this evidence, an earlier investigation indicated that frontal and posterior parietal areas share similar functional properties, thus suggesting that the parietal region is not the sole area involved in the generation of motor commands appropriate for carrying the hand to a visual target.

Collectively, results from these studies indicate that coding visual guided reaching requires the integration of multisensory information into common or comparable frames of reference, and that this multimodal fusion relies on the combinatorial properties of the parietal and frontal reach neurons.

Another important issue that has been studied by researchers pertains to the investigation of the “early” mechanisms of reaching. Of relevance is to understand the temporal evolution of the information processing flow from vision to reaching movement and the stage at which the convergence of multimodal reach-related signals occurs. In a recent study, mechanisms underlying the early formation of motor commands for reaching in the parietal cortex were investigated. Results not only confirmed previous evidence suggesting that neurons within the posterior parietal cortex encode both visual and eye-related signals, but also indicated that their activity is modulated by arm-related information at very early stages of the reach coding. Overall, it seems that many parameters connected to visually-guided reaching, such as visual stimuli, oculomotor behavior, and arm motor behavior, affect neuronal activity at an early stage of the visuomotor processing.

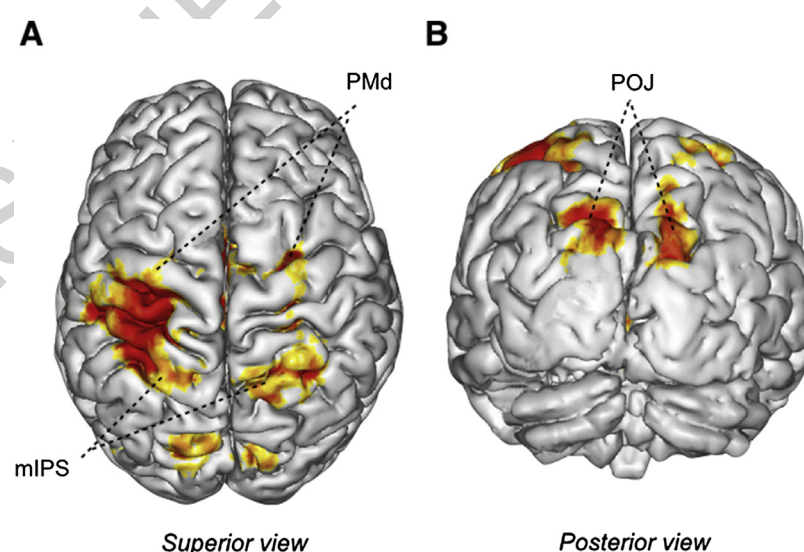
s0025 Reaching in Humans

s0030 Neuropsychological Evidence

p0045 The role of the human posterior parietal cortex in reaching has been well documented by neuropsychological studies conducted on patients suffering from optic ataxia, a specific disruption of visually-guided hand movements in which misreaching occurs mainly for targets presented in the peripheral visual field, and in most cases not for targets presented in the central vision. Thus, it is possible that two neural systems are engaged in reaching to targets in the peripheral versus central visual field. Nevertheless, these patients are usually able to saccade to targets or to accurately reach towards targets presented on their own bodies, suggesting that optic ataxia is not a pure sensory or a motor disorder. The lesions underlying optic ataxia were classically localized within the posterior parietal cortex, in particular along the intraparietal sulcus (IPS), sometimes extending into the IPL and SPL. A more recent neuropsychological study, in which parietal lesions of optic ataxic patients were compared with parietal lesions of patients who were not diagnosed with optic ataxia, indicated that specific parietal areas associated with this disorder, besides the IPS, are the medial parieto-occipital junction (mPOJ), the superior occipital gyrus and the SPL (Fig. 1B). However, the variability of deficits that arises from large and extensive lesions of cortex in optic ataxia patients remains an important limitation of the neuropsychological data. Recent evidence considering the lesion overlap of eleven patients with optic ataxia, showed that the areas of damage mainly involved the bilateral POJ, IPS and the precuneus in the SPL.

s0035 Neuroimaging and Transcranial Magnetic Stimulation

p0050 There are many ways to reach an object. Various studies had subjects either reach to touch an object with their index finger, reach to touch an object with their knuckles, or reach-to-grasp an object. These tasks differ in their demands and may therefore produce results that are not directly comparable. Functional Magnetic Resonance Imaging (fMRI) studies of different reaching types typically report activations in multiple posterior parietal and frontal areas, including the medial IPS and the precuneus in the SPL. Besides the primary motor (M1) and somatosensory activations that are entirely contralateral, the dorsomedial parietofrontal "reaching" activation is bilateral, though stronger in the contralateral hemisphere. Although characterized by this methodological variability, results from human neuroimaging studies appear to fit nicely with the neuropsychological findings in optic ataxia. Furthermore, an fMRI study in healthy participants suggested the existence of two distinct neural circuits supporting reaching in the central compared with the peripheral visual field. The first circuit, specific for reaching in central vision, consisted of a restricted network including the bilateral medial IPS and the most caudal part of the left PMd (Fig. 2A). The second system, specific for reaching in peripheral vision, recruited the same network with the addition of two other areas: the bilateral mPOJ and the rostral part of the PMd in both hemispheres (Fig. 2B). These findings indicate that reaching to targets in the peripheral visual field might engage a more extensive cortical network, explaining well the reaching deficits observed in patients with optic ataxia. However, it should be noted that reaching in the central and peripheral conditions reflect the tasks of differing difficulty, and that several other studies did not replicate this distinction. Thus, recent study showed that when the target object is visible,



f0015 **Figure 2** Panel "A" represents brain activity within the human neural circuit specific for reaching in central vision as identified by Prado, J., Clavagnier, S., Otzenberger, H., Scheiber, C., Perenin, M.T., 2005. Two cortical systems for reaching in central and peripheral vision. *Neuron* 48, 849–858. This circuit comprises the medial intraparietal sulcus (mIPS) and the dorsal premotor cortex (PMd). Panel "B" shows brain activity within the parieto-occipital junction (POJ), an area specific for reaching in peripheral vision.

4 Reaching and Grasping

both peripheral and central visual field conditions activate the same network consisting of POJ, IPS and SPL areas—with increased signals during reaching to visible peripheral targets.

p0055 Parietal cortical networks for reaching seem to be differentially activated depending on the sensory conditions that include visual and proprioceptive feedback. A recent study compared reaching movements towards external peripheral targets, with or without visual feedback, with eye movements (ie, saccades). Whereas visual reaching involved both visual feedback and proprioception, nonvisual reaching required only the proprioceptive feedback. The results showed that the anterior precuneus of the SPL, extending into medial IPS and IPL, were active in both visual and nonvisual reaching, whereas a more posterior region, the parieto-occipital sulcus (POS), was more active for reaching when visual feedback was available. Additionally, although less strong, saccade activations overlapped with the reaching network. Thus, it was proposed that the anterior parietal regions receive proprioceptive signals to guide reaching and respond to hand movements, whereas the more posterior parietal regions rely more on visual feedback and respond to both hand and eye movements. Both types of reaching activated the frontal regions, including the PMd, the frontal eye fields, the supplementary and cingulate motor cortices and a smaller region in PMv.

p0060 The frontoparietal pattern of activation for reaching seems to be present not only for executed reaching movements, but also for the observed as well as imagined reaching movements. A functional overlap between execution, observation and imagery of reaching was found in frontoparietal regions of PMd, the SPL and the IPS. Overall, the fMRI findings are consistent with the literature in macaque pointing to the dorsomedial frontoparietal circuit specialized for reaching.

p0065 Many studies have focused on the important role of the parieto-occipital (PO) regions in reaching (Fig. 1B). For example, the contralateral superior parieto-occipital cortex (SPOC) was implicated in computing whether an object is within or outside the reaching distance, with the activations greater when the target object was in the peripersonal space. SPOC has gained substantial attention in the visuomotor literature, with possible roles including the specification of reaching goals in visual coordinates, coding extrinsic as well as intrinsic object properties, and specifying reach direction and hand/wrist orientation.

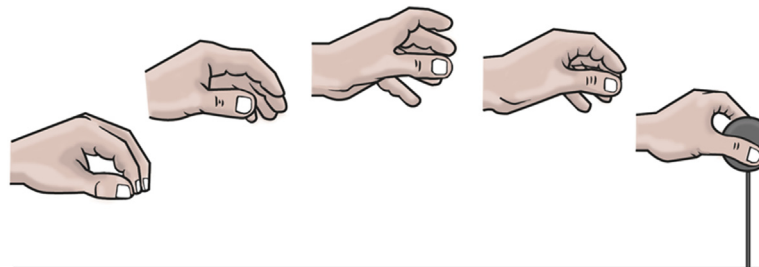
p0070 Using Transcranial Magnetic Stimulation (TMS) over the human posterior parietal cortex, a technique that induces temporary and circumscribed virtual lesions, it has been produced a tendency to reach closer towards fixation, and the inability to correct in order to compensate for jumps in target location and learn new movements trajectories. When TMS was applied over SPOC it produced endpoint errors towards the fixation point with no effect on saccades, assigning to this region the coding of peripheral reach goals. TMS over the angular gyrus close to the IPS produced increased endpoint variability for reaching and decreased accuracy for contralateral saccades, pointing to the overlapping maps for eye and hand movement plan in this brain area. Again, these results confirm the prominent role played by the posterior parietal cortex in the planning and execution of reaching movements.

s0040 Grasping

p0075 Grasping is coded in terms of changes in grip aperture—the separation between the thumb and the index finger, and hand-shaping—the posture assumed by all digits along the reaching action. During a reach-to-grasp movement, a progressive opening of the grip occurs first, with straightening of the fingers, followed by a gradual closure of the grip until it matches the object's size and shape (Fig. 3). As discussed in the following sections, a surge in prehension research is forming the basis for unraveling the neural circuits underlying this action. The canonical dorsolateral parietofrontal network was thought to be chiefly involved. Nevertheless, recent evidence suggests that both dorsolateral and dorsomedial networks support reach-to-grasp movements. Dorsomedial pathway contains neurons not only sensitive to the reach direction, but also to the orientation and shape of a target object, as well as the hand orientation and grip formation necessary for stable and efficient grasping. It has been proposed that the relative contribution of the dorsomedial and dorsolateral networks may instead reflect different requirements of specific movements in terms of planning, online control, or the integration of perceptual information.

s0045 Grasping in the Monkey

p0080 By means of single-cell recordings three specific areas involved in grasping have been uncovered in the cortex of the monkey brain: the primary motor cortex (F1), the ventral premotor cortex (F5), and the anterior intraparietal sulcus (AIP; Fig. 1C). In terms of



f0020 **Figure 3** Example of how the hand pre-shapes during reaching to grasp the target object.

neural mechanisms, performing a successful grasping action depends primarily on the integrity of the primary motor cortex (F1). Lesion of this area in monkeys produces a profound deficit in the control of individual fingers and consequently disrupts normal grasping.

p0085 Another fundamental process for a successful grasp involves a transformation of the visually mapped intrinsic properties of the object (eg, size, shape) into motor actions. Compared to the dorsomedial circuit for reaching, a dorsolateral frontoparietal neural circuit is thought to be involved in visuomotor transformations for grasping in monkeys. This network is composed of the areas F5 and AIP. Area F5 forms the rostral part of the monkey ventral premotor cortex (PMv), while AIP is a small zone within the rostral part of the posterior bank of the intraparietal sulcus, directly connected with area F5.

p0090 On the basis of the functional roles of neurons in areas AIP and F5, a model has been developed in which area AIP provides multiple descriptions of three-dimensional objects for the purpose of manipulation, whereas area F5 is mainly involved in selecting the most appropriate motor prototype from a motor vocabulary, for example, the type of grip that is effective in interacting with a target object. Confirmation that the AIP/F5 circuit is likely to be relevant for grasping has also been derived by reversible inactivation of each of these areas independently in the monkey. Inactivation of either AIP or F5 markedly impaired hand shaping during reaching, and the hand posture was inappropriate for the object size and shape.

p0095 Recent evidence suggests that the dorsomedial network, composed of monkey PMd and PRR (V6A)—previously implicated in reaching movements only, contains grasp-selective neurons specialized for the grip type, hand orientation and shaping the hand according to the target object's visual properties. It has been suggested that while dorsolateral circuit might be crucial for integrating visual information about the object into motor plans for efficient grasping, the dorsomedial pathway might play a role in reach and grasp coordination necessary for efficient grasping.

p0100 Somatic receptors in muscles, joints and skin provide information regarding the current posture of the hand and its location and orientation with respect to potential targets for grasping. To investigate the conjunction of visual and somatic processing, one study compared the timing of spike trains obtained by single-unit recording in the somatosensory cortex (SI) and the anterior intraparietal cortex (AIP) of the same animals during a reach-to-grasp task. The shape of the target object influenced the response of cells in AIP. Neurons in SI typically responded later than those in AIP, showing a significant increase in firing rates only after the hand touched the object, and peaking when grasping was secure. Further, SI neurons rarely differentiated the shape of the grasped object in the manner that occurred in AIP neurons.

s0050 Grasping in Humans

s0055 Neuropsychological Evidence

p0105 The first evidence for specialised grasping circuits in the human brain came mainly from the neuropsychological literature. As in the monkey, lesions of the human primary motor cortex or corticospinal fibers profoundly disrupt grasping. Such lesions typically lead to grasping movements initially characterized by the loss of independent finger movement, although synergistic movements of all fingers (a power grip) remain intact.

p0110 In terms of the human-monkey homology, there is evidence that the anterior intraparietal sulcus in the posterior parietal cortex is a homologue of monkey AIP (termed hAIP), having a crucial role in human grasping. It has been suggested that the area responsible for grasping is confined to the hAIP contralateral to the impaired hand (Fig. 1D). In line with the results obtained from AIP inactivation in monkeys, human patients with hAIP lesions have deficits in grasping, whereas reaching remains relatively intact.

p0115 The evidence that posterior parietal lobe is important for grasping comes from patients with optic ataxia who exhibit abnormally large finger grip aperture during reach-to-grasp movements, with the usual correlation between the maximum grip aperture and the object size missing. Also, various patients with SPL damage have been described having specific deficits in the control of grasping. Patient V.K., for example, showed an apparently normal early phase of hand opening during attempts to grasp an object, but the on-line control of grip aperture quickly degenerated, resulting in numerous secondary peaks in the grip aperture profile, rather than a single peak typical of a healthy subject. Another patient, A.T., with extensive damage to the SPL, secondary visual areas, and some damage to the IPL, showed exaggerated anticipatory opening of the fingers with poor correlation with object size, resulting in awkward grasps. However, this deficit was much less marked if "laboratory" objects, such as wooden blocks, were replaced with familiar objects, such as a lipstick. Thus, in the case of commonly used objects, prior knowledge and cognitive cues can be used to determine the size of an object, suggesting that the meaning attached to an object might modulate classic grasping circuits.

s0060 Evidence From Neuroimaging and TMS

p0120 Brain imaging experiments in humans have investigated the existence and localization of cortical circuits for grasping similar to those described in monkeys. Early attempts to use brain imaging to identify the human functional anatomy underlying the generation of goal-directed arm movements during the action of reaching and grasping were conducted using positron emission tomography (PET). These early studies investigated differences between grasping movements of different types, compared to hand transport actions such as pointing, reaching to touch, or just observing the target object. Together they implicate important regions of the frontal and parietal lobes such as the contralateral primary motor cortex, the bilateral premotor cortex (PMC), the prefrontal cortex (PFC), and the posterior parietal cortex (PPC) including hAIP and IPL regions (Fig. 1D).

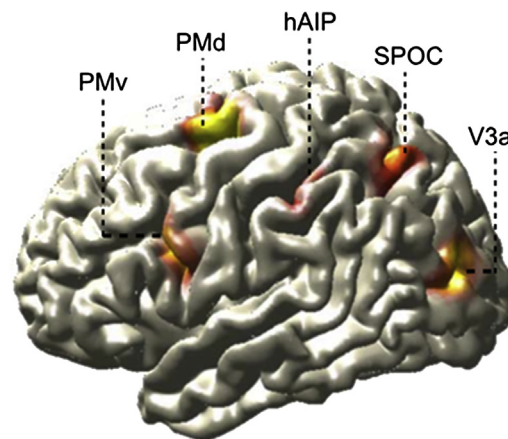


Figure 4 Cerebral activity over occipital, parietal and frontal regions during visually guided grasping in humans, as reported in Grol et al., (2007). Abbreviations: PMd, dorsal premotor cortex; PMv, ventral premotor cortex; hAIP, anterior intraparietal sulcus.

Studies conducted with fMRI provide superior spatial resolution to PET imaging and eliminate many of the possible confounds that characterized the earlier PET studies.

fMRI studies mostly focused on exploring a neural network supporting grasping in the human brain similar to the classic AIP-F5 pathway in monkey. When subjects have to perform three different grasping actions, starting with the subjects executing different types of grasps according to the target object's properties (power grip or precision grip), subjects imitating a pantomime action, or subjects imitating a viewed hand grasping an object, a common frontoparietal network activates. The areas that are active are consistent with the monkey AIP-F5 visuomotor circuit, and include the hAIP, the PMv (equivalent to F5) and the PMC. In line with recent findings in the monkey, fMRI evidence in humans shows that the dorsomedial "reach" circuit (PMd – SPL) is also active during preparation and execution of reach-to-grasp movements (Fig. 4). Bilateral PMd, SPOC and precuneus seem to play a role in coding hand orientation for grasping movements, and coordinating different components of reach-to-grasp movements. Recently, a gradient between reaching and grasping activation was described in the posterior parietal cortex, with greatest reach activation located in the precuneus and SPL, and greatest grasp activity noted in the hAIP. Recent fMRI adaptation study further showed that the role of hAIP is in coding intrinsic object properties (eg, object size) relevant for hand shaping and force scaling, whereas dorsomedial components, ie, PMd, SPOC and precuneus coded intrinsic as well as extrinsic object properties (eg, location), relevant for both the reaching and the grasping phase.

Functional MRI brought important insights into the crucial role of bilateral hAIP in reach-to-grasp movements, an area that is active even when no reaching component is involved. One study used an alternating task design, in which grasping a rectangular object of varying orientations was used as the activation condition, while pointing towards the object was used as the baseline condition. The results showed a specific activation of the lateral bank of hAIP in grasping tasks, together with activations including the contralateral sensorimotor cortex, bilateral PMC, and the PPC. The activated part of hAIP is the same area in which lesions in humans, and chemical deactivation in monkeys, lead to grasping deficits (Fig. 1D). The importance of hAIP was further confirmed by studies that used a region of interest approach and event-related designs. For example, subjects were presented with a diverse and unpredictable sequence of objects (rectangular shapes of varied length and orientation) using custom equipment "the grasp-aratus," and had to reach towards the long axis of the objects and grasp them using a precision grip. The results provided strong evidence that hAIP contributes to the ability to execute precision grasping.

When reach-to-grasp movements are performed towards objects of different size, subjects naturally use precision grip to grasp small objects, and power grip to grasp large objects. Activity in the hAIP seems to be tuned to the type of grip, since significant activity has been detected for precision but not for power grip movements. Combining natural and constrained grip types (precision versus power grip) on the same sized objects (small or large) showed that this differential hAIP activity depended on distinct hand postures and the grasp type, and not on different sizes of the objects. Thus, the type of the grasp used modulates the functional brain architecture during reach-to-grasp movements, and significantly affects the hAIP activity. This is in line with the recent finding from fMRI study that explored causal influence that frontoparietal regions exert over another. Effective connectivity in the dorsolateral circuit (hAIP-PMv) increased during grasping and manipulation of small objects, whereas effective connectivity in the dorsomedial circuit (SPOC-PMd) increased during grasping and manipulation of large objects (Fig. 4). Other factors that can modulate brain activity during grasping movements include the hand used (left or right) and handedness. It was observed that the right PMd exhibits handedness-independent role in monitoring hand shaping during precision grip, unlike the hAIP activity that varies depending on handedness.

Recently it has been shown that the planning and online monitoring/control of grasping activate different non-overlapping regions in the frontal and posterior parietal cortex. Action planning includes processes occurring before the movement initiates (goal specification, target identification and selection, timing, computation of target object's properties), while online control monitors the movement during execution by integrating visual and proprioceptive feedback with a forward model. Planning

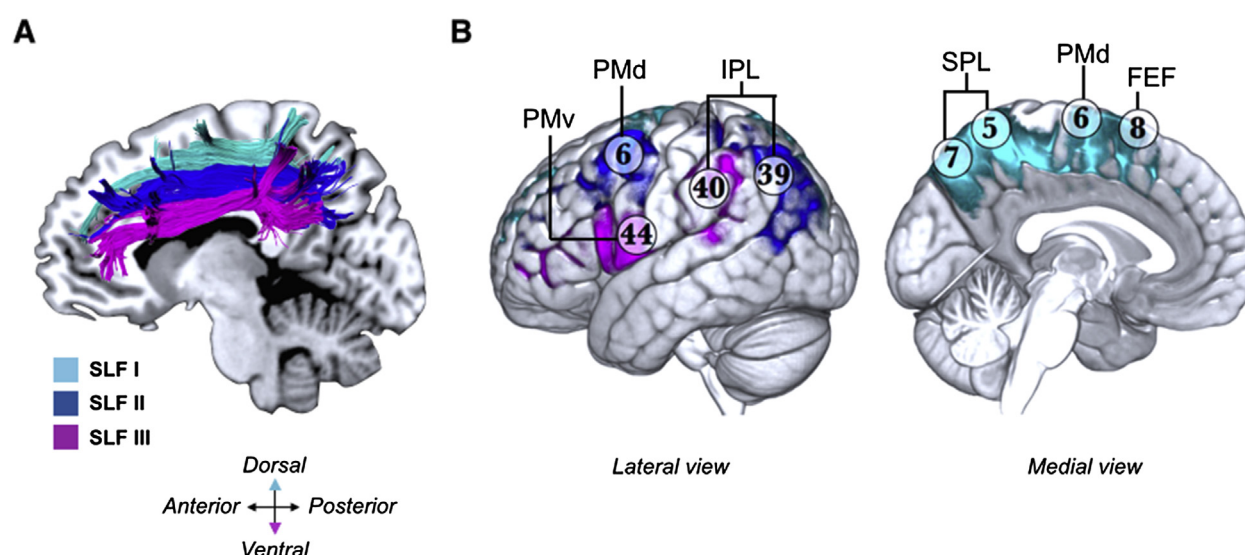


Figure 5 (A) Virtual DTI tractography dissection of the fronto-parietal connections of the superior longitudinal fasciculus (SLF) showing the most dorsal branch in light blue (SLF I), the middle component in navy blue (SLF II), and the ventral component in violet colour (SLF III); (B) Cortical projections of the fronto-parietal pathways adapted from Rojkova et al., with numbers denoting Brodmann cortical areas. Abbreviations: PMd, dorsal premotor cortex; PMv, ventral premotor cortex; IPL, inferior parietal lobule; SPL, superior parietal lobule; FEF, frontal eye fields.

and control activity showed a rostral–caudal distinction in the frontal lobes, with more prefrontal and premotor regions involved in pre-movement planning and primary motor regions active during online control. In the parietal lobes, the planning of reach-to-grasp involved the middle intraparietal, posterior medial parietal and SPOC regions, whereas online control involved separate regions of the SPL and supramarginal gyrus of the IPL.

Recent work has shown that TMS has the potential to reveal important facts about the neural networks that mediate grasping. For instance, repetitive TMS stimuli applied over the left SPL as participants reached to grasp objects changing in size, indicate that this area might be crucial for the on-line control of grasping. Consistent with recent fMRI evidence of reaching-related activation in the SPOC and grasping-related activations in the hAIP of the PPC, a recent paired pulse TMS study showed greater functional interaction between M1 and hAIP during grasping, and between M1 and SPOC during reaching movements. Others showed that TMS to hAIP disrupts the grasp but not the reach component of reach-to-grasp movement, further highlighting the crucial role of this region in grasping phase. TMS research also highlighted potentially different roles for the PMv and the PMd in grasping. When TMS is applied over the PMv, the grasping phase in a grasp-to-lift task is disrupted. However, when the PMd is temporarily lesioned, the coupling between the grasping and the lifting phase is disrupted by delaying the recruitment of the proximal muscles involved in the lifting phase. A subsequent study showed that the PMv might be important for processing target object's intrinsic properties that are then implemented through motor cortex for efficient grasping movement.

The literature on cortical correlates underlying prehension is extensive; however understanding the role of white matter in grasping is still lacking. Diffusion MRI tractography is nowadays extensively used to explore distinct white matter networks in vivo. A recent study combining bifocal TMS and tractography in humans suggested that connections between frontal and parietal regions, consisting of the three branches of the superior longitudinal fasciculus (SLF I-III; Fig. 5A) might be important in planning reach-to-grasp movements. The most dorsal branch SLF I connects the dorsomedial parietofrontal “reach” regions: the precuneus and the SPL with the superior frontal regions, while the middle branch SLF II connects the IPL (angular gyrus, IPS) with the PMd. The most ventral branch SLF III links the classical dorsolateral “grasp” network: the IPL and the PMv (Fig. 5B). Other findings show that bilateral SLF II and SLF III connections correlate with kinematics of reach-to-grasp movements. Right-hemispheric advantage at the level of the SLF II, and larger SLF III in both hemispheres, were associated with faster reach-to-grasp movements. Also, the right SLF II was crucially involved in the reach-grasp coordination and the visuomotor transformation necessary for successful final hand position.

The future of prehension research might lie in multimodal imaging, combining fMRI and TMS data with high temporal resolution (EEG and MEG) and structural connectivity (diffusion MRI) approaches, in order to decipher the dynamic nature of prehension movement in terms of temporal evolution, and functional and structural brain correlates.

Further Reading

- Andersen, R.A., Andersen, K.N., Hwang, E., Hauschild, M., 2014. Optic ataxia: from Balint's syndrome to the parietal reach region. *Neuron* 81 (5), 967–983.
- Begliomini, C., Caria, A., Grodd, W., Castiello, U., 2007. Comparing natural and constrained movements: new insights into the visuomotor control of grasping. *PLoS One* 2 (10), e1108.

8 Reaching and Grasping

- Bennett, K.M.B., Castiello, U., 1994. *Insights into the Reach to Grasp Movement*. Elsevier, Amsterdam.
- Castiello, U., 2005. The neuroscience of grasping. *Nat. Rev. Neurosci.* 6, 726–736.
- Cattaneo, L., Voss, M., Brochier, T., et al., 2005. A cortico-cortical mechanism mediating object-driven grasp in humans. *Proc. Natl. Acad. Sci.* 102, 898–903.
- Culham, J.C., Valyear, K.F., 2006. Human parietal cortex in action. *Curr. Opin. Neurobiol.* 16, 1–8.
- Fadiga, L., Craighero, L., 2004. Electrophysiology of action representation. *J. Clin. Neurophysiol.* 21, 157–169.
- Filimon, F., 2010. Human cortical control of hand movements: parietofrontal networks for reaching, grasping, and pointing. *Neuroscientist* 16 (4), 388–407.
- Fogassi, L., Gallese, V., Buccino, G., et al., 2001. Cortical mechanism for the visual guidance of hand grasping movements in the monkey: a reversible inactivation study. *Brain* 124, 571–586.
- Frey, S.H., Vinton, D., Norlund, R., Grafton, S.T., 2005. Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Cogn. Brain Res.* 23, 397–405.
- Galletti, C., Kutz, D.F., Gamberini, M., Breveglieri, R., Fattori, P., 2003. Role of the medial parieto-occipital in the control of reaching and grasping movements. *Exp. Brain Res.* 153, 158–170.
- Glover, S., Miall, R.C., Rushworth, M.F.S., 2005. Parietal rTMS selectively disrupts the initiation of on-line adjustments to a perturbation of object size. *J. Cogn. Neurosci.* 17, 124–136.
- Glover, S., Wall, M.B., Smith, A.T., 2012. Distinct cortical networks support the planning and online control of reaching-to-grasp in humans. *Eur. J. Neurosci.* 35 (6), 909–915.
- Grafton, S.T., 2010. The cognitive neuroscience of prehension: recent developments. *Exp. Brain Res.* 204 (4), 475–491.
- Grol, M.J., Majdandžić, J., Stephan, K.E., Verhagen, L., et al., 2007. Parieto-frontal connectivity during visually guided grasping. *J. Neurosci.* 27 (44), 11877–11887.
- Jeannerod, M., Arbib, A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320.
- Karnath, H.O., Perenin, M.T., 2005. Cortical control of visually guided reaching: evidence from patients with optic ataxia. *Cereb. Cortex* 15, 1561–1569.
- Konen, C.S., Kastner, S., 2008. Representation of eye movements and stimulus motion in topographically organized areas of human posterior parietal cortex. *J. Neurosci.* 28 (33), 8361–8375.
- Martin, J.A., Karnath, H.O., Himmelbach, M., 2015. Revisiting the cortical system for peripheral reaching at the parieto-occipital junction. *Cortex* 64, 363–379.
- Porter, R., Lemon, R.N., 1993. *Corticospinal Function and Voluntary Movement*. Oxford University Press, Oxford.
- Prado, J., Clavagnier, S., Otzenberger, H., Scheiber, C., Perenin, M.T., 2005. Two cortical systems for reaching in central and peripheral vision. *Neuron* 48, 849–858.
- Rizzolatti, G., Luppino, G., 2001. The cortical motor system. *Neuron* 31, 889–901.
- Stark, E., Asher, I., Abeles, M., 2007. Encoding of reach and grasp by single neurons in premotor cortex is independent of recording site. *J. Neurophysiol.* 97 (5), 3351–3364.
- Wing, A.M., Haggard, P., Flanagan, J.R., 1996. *Hand and Brain: The Neurophysiology and Psychology of Hand Movements*. Academic Press, San Diego.