

Precision grasping in humans: from motor control to cognition

Etienne Olivier¹, Marco Davare¹, Michael Andres¹ and Luciano Fadiga^{2,3}

In the past decade, functional neuroimaging has proved extremely useful in mapping the human motor circuits involved in skilled hand movements. However, one major drawback of this approach is the impossibility to determine the exact contribution of each individual cortical area to precision grasping. Because transcranial magnetic stimulation (TMS) makes it possible to induce a transient 'virtual' lesion of discrete brain regions in healthy subjects, it has been extensively used to provide direct insight into the causal role of a given area in human motor behaviour. Recent TMS studies have allowed us to determine the specific contribution, as well as the timing and the hemispheric lateralisation, of distinct parietal and frontal areas to the control of both the kinematics and dynamics of precision grasping. Moreover, recent researches have shown that the same cortical network may contribute to language and number processing, supporting the existence of tight interactions between processes involved in cognition and actions. The aim of this paper is to offer a concise overview of recent studies that have investigated the neural correlates of precision grasping and the possible contribution of the motor system to higher cognitive functions such as language and number processing.

Addresses

¹ Laboratory of Neurophysiology, School of Medicine, Université catholique de Louvain, Brussels, Belgium

² University of Ferrara, Italy

³ The Italian Institute of Technology, Genova, Italy

Corresponding author: Olivier, Etienne (etienne.olivier@uclouvain.be), Davare, Marco (marco.davare@uclouvain.be), Andres, Michael (michael.andres@psp.ucl.ac.be) and Fadiga, Luciano (fdl@unife.it)

Current Opinion in Neurobiology 2007, **17**:644–648

This review comes from a themed issue on
Motor systems
Edited by Roger Lemon and Paul Bolam

Available online 11th March 2008

0959-4388/\$ – see front matter

© 2008 Elsevier Ltd. All rights reserved.

DOI [10.1016/j.conb.2008.01.008](https://doi.org/10.1016/j.conb.2008.01.008)

Introduction

'The special relationship we indubitably enjoy with the material universe is to a very great extent the result of the special virtues of our hands' [1]. Fine manipulative skills and precise tool use are unique attributes of the human species. Although some non-human primates are also able to perform sophisticated hand movements, including the use of simple tools, the human manipulative superiority

arises most probably from the intimate interactions between motor skills and higher cognitive functions.

In the past decade, functional neuroimaging studies have reopened several major questions in human motor neuroscience. One important issue is the neural correlate of skilled hand movements and, particularly, of precision grasping. Neuroimaging studies have shown that, in addition to the corticospinal system [2], precision grasping crucially involves an extensive cortical network, including the dorsal (PMd) and ventral (PMv) premotor cortex and the supplementary motor area (SMA) and a mosaic of areas located in the intraparietal (IP) sulcus [3–5]. When using tools or manufactured objects, the activated areas extend to the convexity of the inferior parietal lobule [6–8]. Although it is sensible to assume that each motor-related area has a specific contribution to precision grasping, neither functional imaging studies, nor clinical studies have allowed us to answer this question definitely. Because transcranial magnetic stimulation (TMS) may be used to induce transient 'virtual lesions' of discrete brain areas in healthy subjects while performing a motor task [9], TMS has provided invaluable insights into neural mechanisms responsible for motor control. Several recent TMS studies have allowed us to determine how various parietal and frontal areas contribute to the visuomotor transformations underlying grasping movements.

Another intriguing finding in functional neuroimaging is the considerable overlap that exists between the cortical areas controlling skilled hand movements and those involved in higher cognitive functions, such as language and number processing. These results have challenged the view that the motor circuits are exclusively dedicated to controlling actions and have provided new insights into the deeply rooted interactions between actions and cognition.

The present review offers an overview of recent studies that have shed light on the neural correlates of precision grasping and on the possible contribution of this system to higher cognitive functions such as language or number representation.

Neural correlates of hand preshaping

When reaching for an object, one crucial step is to adjust the hand posture to its intrinsic features (size, shape and orientation) [10,11]. Both electrophysiological studies in monkeys [12–15] and functional neuroimaging in humans [3,16,17,18] have shown that a cortical circuit consisting of the anterior part of the IP sulcus (AIP) connected to PMv is responsible for processing

visuospatial information about the object [14,19]. Within that ‘grasping circuit’, the exact contribution of AIP and PMv is still unclear and reversible inactivation of these two areas in monkeys have failed to differentiate their role in precision grasping [20,21]. Moreover, it is noteworthy that a recent neuroimaging study has questioned the existence of such a ‘grasping circuit’ dedicated to grasping movements [18**].

Two recent TMS studies have investigated the role of AIP and PMv in humans [22**,23*] by inducing a transient virtual lesion of either area in healthy subjects performing a standard grip-lift task. It has been shown that a bilateral lesion of AIP was necessary to alter the preshaping of either hand, suggesting that, in humans, both AIP contribute crucially to hand shaping, irrespective of the hand used [22**]. This finding is compatible with neuroimaging studies showing a bilateral recruitment of AIP in tasks requiring unimanual movements [3–5,8,19,24], as already suggested by monkey experiments [25]. Other recent TMS studies have also highlighted the role of AIP in controlling the hand preshaping ‘on-line’, when an ‘error’ was detected during the hand transport, for example when the object size or orientation was unexpectedly changed after movement initiation [26,27**]. This indicates that AIP not only contributes to the hand preshaping during movement preparation, but is also involved in monitoring errors in hand conformation on-line.

In contrast to AIP, a unilateral lesion of either PMv was found sufficient to impair selectively the preshaping of the right dominant hand, indicating that both PMv are necessary to perform visuomotor transformation of intrinsic features of the object [11,19], a finding consistent with neuroimaging studies demonstrating a bilateral activation in both PMv when subjects manipulate [3] or grasp an object [4,5]. Besides its contribution to hand shaping, PMv was also found to influence the timing of the intrinsic hand muscle recruitment. However, we found that only lesions of the left PMv altered the recruitment of intrinsic muscles of the right hand, in accordance with monkey experiments showing that an inactivation of PMv influences the timing of the agonist–antagonist muscle recruitment in the contralateral hand [28]. These results suggest that, at an early stage of the movement preparation, both PMv are involved in the visuomotor transformations, leading to the appropriate hand preshaping and that, once a given hand is selected to perform the movement, only the contralateral PMv is involved in the grasping implementation.

To sum up, it is sensible to assume that AIP feeds PMv with visuospatial information about intrinsic properties of the object, whereas PMv implements the motor aspect of the grasp component; then a feedback loop from PMv to AIP permits to compute any mismatch between the grasp

conformation and the object intrinsic properties if a change in object orientation occurs [14]. This view is compatible with the high connection probability found between PMv and AIP in humans [29**] and with the fact that grasping small objects led to an increase in the effective connectivity between these two areas, probably because fine movements highly rely on on-line control [18**]. Finally, it has been shown that, during movement preparation, the contribution of AIP to hand shaping occurs about 50 ms before that of PMv, supporting the classical view that AIP and PMv interact serially [11,19].

Neural correlates of grip force control

Another crucial parameter that has to be controlled once the fingers are positioned around the centre of mass of the object is the force exerted on this object. The so-called grip force has to be precisely scaled in order to prevent the object from slipping or from being damaged [30]. Scaling the grip force according to the weight and frictional properties of the objects is programmed anticipatorily, an ability thought to rely on internal models [31]. Studies in brain-damaged patients indicate that lesions encompassing parts of the occipital and parietal lobes alter the ability to anticipate the grip forces correctly [32] and patients with cerebellar lesions apply too high grip force, revealing a strategy to compensate for their inappropriate grip force anticipation [33]. These observations suggest that both the parietal cortex and cerebellum are crucially involved in the implementation and/or the storage of the object internal models. Neuroimaging studies have shown that both the cerebellum and the SMA are involved in the grip force adjustment when the object weight changes unpredictably [34,35**], whereas IP areas are rather involved in monitoring the difference between the predicted and the actual object weight, without implementing the corrective motor command [35**].

In particular, it has been shown that TMS-induced lesions of AIP led to an increase in grip force [22**], suggesting that the subjects overestimated the weight of the object, exactly as reported in experiments in which the object is unexpectedly replaced by a lighter one [30]. Interestingly, only a virtual lesion of the left, but not right, AIP produced such an effect. Therefore, it is sensible to assume that the left AIP is involved in the implementation – or the retrieval – of object internal models [31]. Additionally, it has been shown that this process is performed by AIP about 150 ms before the fingers contact the object [22**], namely 100 ms after AIP processed hand preshaping. This corroborates the view of Jenmalm *et al.* that IP areas monitor the mismatch between the anticipated and actual object weight in order to update the internal model and, if required, to trigger a correction [35**]. Importantly, this TMS study of Davare *et al.* [22**] demonstrates that the left hemispheric dominance not only concerns high-level processes such as hand–tool interactions [8,36–38], but also applies to more

elementary aspects of movements, such as the representation of object dynamics.

Precision grasping and higher cognitive function

A recurrent finding in functional neuroimaging over the past decade is the considerable overlap between the cortical areas controlling skilled hand movements and those involved in higher cognitive functions [39], such as language [40^{••}] and number of representations [41–43,44^{••}]. These findings have challenged the view that the ‘grasping circuit’ is exclusively dedicated to controlling actions, suggesting that visuomotor transformations underlying precision grasping are somehow permeable to cognitive processes. Indeed, the frontal and parietal areas involved in grasping movements may also play a role in representing and communicating the content and/or the meaning of actions.

As shown in the previous sections, both AIP and PMv are endowed with specific processing mechanisms that lead to the transformation of visuospatial information about the intrinsic properties of an object into the appropriate hand preshaping. These transformations are revealed by the correlation between the grip aperture (i.e. the distance between the thumb and index finger) and the size of the object to grasp during the transport of the hand. In addition to the object intrinsic properties, Glover *et al.* found that the initial grip aperture for grasping a wooden block was also influenced by the word that participants had to read before movement execution: the grip aperture was larger when reading a word representing a large object (e.g. ‘apple’) and smaller when reading the name of a small object (e.g. ‘grape’) [45[•]]. The programming of grip aperture was also influenced by concepts as abstract as numerical magnitudes, as shown by the effect of small (i.e. 1 or 2) and large digits (i.e. 8 or 9) on imagined [46^{••}] and actual grasp movements [47[•]]. Therefore, it can be assumed that the fronto-parietal circuit responsible for grasping is endowed with processes that automatically take into account the magnitude estimates conveyed by the names of graspable objects or by numbers.

Another fascinating property of the ‘grasping circuit’ is its sensitivity to visual information. Indeed, several monkey studies showed that the hand motor system is activated not only during action execution but also during observation of graspable objects (canonical neurons, [48]), without movement execution, as well as during observation of other individuals performing grasp movements similar to those they encode during active grasp (mirror neurons [49], see also reference [50]). In humans, the sensitivity of motor-related areas to the observation of manipulable objects has been shown by both functional neuroimaging studies [6,51,52] and behavioural experiments (visuomotor priming, [53–55]). Similarly, the existence of a human mirror–neuron system during grasp-

ing observation finds its experimental support in TMS experiments, demonstrating that the corticospinal system becomes facilitated during observation of others’ actions (for a review see reference [56]), and in brain imaging data, showing that the observation of grasping acts performed by other individuals activates a set of cortical areas recruited during the execution of grasping movements (see reference [50] for a review). Altogether, these results suggest that the grasping circuit encodes grasp-related properties in an abstract motor representation that can be accessed either automatically, in the case of object or action observation, or voluntarily, as in the case of action execution or motor imagery [57].

The capacity to represent an action internally in the absence of any motor contingency confers on the grasping circuit a potential influence in the organisation of semantic knowledge about graspable objects and makes this circuit a privileged interface for matching our actions with the actions of others, giving rise to inter-individual communication. In keeping with this assumption, it has been shown that Broca’s area, the frontal area involved in speech production, is also active during non-linguistic motor tasks, such as hand action observation, imitation and motor imagery [50,58,59]. The finding that Broca’s area shares several morphological properties with a subregion of the monkey PMv underlines the need to reconcile cytoarchitectonic and functional mapping of the monkey PMv in order to determine whether this crucial part of the grasping circuit can be considered as a precursor of the cerebral substrate for language in humans [60[•],61^{••}]. Provided that Broca’s area is able to code the characteristics of both our and other’s actions, the involvement of this region in verbal communication could be provocatively considered as an occasional ‘epiphenomenon’, motivated by its premotor origins (see reference [39]).

Acknowledgements

This work was supported by grants from the ‘Fonds Spéciaux de Recherche’ (FSR) of the Université catholique de Louvain, the ‘Fonds de la Recherche Scientifique Médicale’ (FRSM) and the ‘Fondation Médicale Reine Elisabeth’ (FMRE) to EO and by MIUR and EC grants Robot-Cub, Neurobotics and CONTACT to LF. MA is a postdoctoral researcher at the Fonds de la Recherche Scientifique (FRS-FNRS). The authors are grateful to Dr Julie Duqué for her comments on an earlier version of this manuscript.

References and recommended reading

Papers of particular interest, published within the annual period of the review, have been highlighted as:

- of special interest
- of outstanding interest

1. Tallis R: *The Hand: A Philosophical Inquiry In Human Being* Edinburgh: Edinburgh University Press; 2003.
2. Duque J, Thonnard JL, Vandermeeren Y, Sebire G, Cosnard G, Olivier E: **Correlation between impaired dexterity and corticospinal tract dysgenesis in congenital hemiplegia.** *Brain* 2003, **126**:732–747.
3. Binkofski F, Buccino G, Posse S, Seitz RJ, Rizzolatti G, Freund H: **A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study.** *Eur J Neurosci* 1999, **11**:3276–3286.

4. Ehrsson HH, Fagergren E, Forssberg H: **Differential fronto-parietal activation depending on force used in a precision grip task: an fMRI study.** *J Neurophysiol* 2001, **85**:2613-2623.
 5. Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H: **Cortical activity in precision versus power-grip tasks: an fMRI study.** *J Neurophysiol* 2000, **83**:528-536.
 6. Chao LL, Martin A: **Representation of manipulable man-made objects in the dorsal stream.** *Neuroimage* 2000, **12**:478-484.
 7. Johnson-Frey SH, Newman-Norlund R, Grafton ST: **A distributed left hemisphere network active during planning of everyday tool use skills.** *Cereb Cortex* 2005, **15**:681-695.
 8. Culham JC, Valyear KF: **Human parietal cortex in action.** *Curr Opin Neurobiol* 2006, **16**:205-212.
 9. Sack AT: **Transcranial magnetic stimulation, causal structure-function mapping and networks of functional relevance.** *Curr Opin Neurobiol* 2006, **16**:593-599.
 10. Goodale MA, Meenan JP, Bulthoff HH, Nicolle DA, Murphy KJ, Racicot CI: **Separate neural pathways for the visual analysis of object shape in perception and prehension.** *Curr Biol* 1994, **4**:604-610.
 11. Jeannerod M, Arbib MA, Rizzolatti G, Sakata H: **Grasping objects: the cortical mechanisms of visuomotor transformation.** *Trends Neurosci* 1995, **18**:314-320.
 12. Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G: **Object representation in the ventral premotor cortex (area F5) of the monkey.** *J Neurophysiol* 1997, **78**:2226-2230.
 13. Murata A, Gallese V, Luppino G, Kaseda M, Sakata H: **Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP.** *J Neurophysiol* 2000, **83**:2580-2601.
 14. Raos V, Umiltà MA, Murata A, Fogassi L, Gallese V: **Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey.** *J Neurophysiol* 2006, **95**:709-729.
 15. Umiltà MA, Brochier TG, Spinks RL, Lemon RN: **Simultaneous recording of macaque premotor and primary motor cortex neuronal populations reveals different functional contributions to visuomotor grasp.** *J Neurophysiol* 2007.
 16. Begliomini C, Wall MB, Smith AT, Castiello U: **Differential cortical activity for precision and whole-hand visually guided grasping in humans.** *Eur J Neurosci* 2007, **25**:1245-1252.
- An fMRI study where the authors investigate whether the cortical activation in AIP may reflect the relationship between object shape and hand configuration, as shown in monkeys. Interestingly, their results show a different degree of activation depending on the type of hand grasping.
17. Frey SH, Vinton D, Norlund R, Grafton ST: **Cortical topography of human anterior intraparietal cortex active during visually guided grasping.** *Brain Res Cogn Brain Res* 2005, **23**:397-405.
- An interesting fMRI study showing that grasping complex objects activates, consistently across subjects, a region located at the junction of the intraparietal and the post-central sulci. That region, called aIPS, plays a key role in the visuomotor transformations involved in grasping and is the homologue in the human brain of the macaque area AIP. The authors also provide an interesting meta-analysis of fMRI coordinates of the AIP activation during grasping movements.
18. Grol MJ, Majdandzic J, Stephan KE, Verhagen L, Dijkerman HC, Bekkering H, Verstraten FA, Toni I: **Parieto-frontal connectivity during visually guided grasping.** *J Neurosci* 2007, **27**:11877-11887.
- An original and inspiring view on the organisation of the parieto-frontal circuits underlying visually-guided movements. This study is based on the quantification of the modulation of the effective parieto-frontal connectivity. The authors argue against the existence of dedicated circuits for reaching and grasping. Rather they suggest that the increased effective connectivity in the AIP-PMv circuit while grasping small objects reveals a high degree of on-line control requirement. Grasping large objects led to an increased coupling in the so-called reaching circuit (V6A-PMd).
19. Castiello U: **The neuroscience of grasping.** *Nat Rev Neurosci* 2005, **6**:726-736.
 20. Fogassi L, Gallese V, Buccino G, Craighero L, Fadiga L, Rizzolatti G: **Cortical mechanism for the visual guidance of hand grasping movements in the monkey: a reversible inactivation study.** *Brain* 2001, **124**:571-586.
 21. Gallese V, Murata A, Kaseda M, Niki N, Sakata H: **Deficit of hand preshaping after muscimol injection in monkey parietal cortex.** *Neuroreport* 1994, **5**:1525-1529.
 22. Davare M, Andres M, Clerget E, Thonnard JL, Olivier E: **Temporal dissociation between hand shaping and grip force scaling in the anterior intraparietal area.** *J Neurosci* 2007, **27**:3974-3980.
- A TMS study showing that, during movement preparation, AIP deals, at different delays, with two distinct movement parameters, namely the shape and weight of the object to be grasped. In addition, this study demonstrates that the lateralisation of these two processes is strikingly different.
23. Davare M, Andres M, Cosnard G, Thonnard JL, Olivier E: **Dissociating the role of ventral and dorsal premotor cortex in precision grasping.** *J Neurosci* 2006, **26**:2260-2268.
- A TMS study showing that, in humans, a virtual lesion of PMv, performed during movement preparation, impairs the preshaping of the hand, estimated by measuring the fingertip position on the object to be grasped. A lesion of PMd performed 100 ms later alters the coupling between the grip and lift components of grasping movements
24. Culham JC, Danckert SL, DeSouza JF, Gati JS, Menon RS, Goodale MA: **Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas.** *Exp Brain Res* 2003, **153**:180-189.
 25. Sakata H, Taira M, Murata A, Mine S: **Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey.** *Cereb Cortex* 1995, **5**:429-438.
 26. Glover S, Miall RC, Rushworth MF: **Parietal rTMS disrupts the initiation but not the execution of on-line adjustments to a perturbation of object size.** *J Cogn Neurosci* 2005, **17**:124-136.
 27. Tunik E, Frey SH, Grafton ST: **Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp.** *Nat Neurosci* 2005, **8**:505-511.
- An interesting TMS study showing that AIP is causally involved in the on-line control of grasping movements. By using a clever paradigm, the authors show that depending on the movement goal, either the grasp aperture or the wrist orientation could be altered by virtual lesions of AIP.
28. Matsumura M, Sawaguchi T, Oishi T, Ueki K, Kubota K: **Behavioral deficits induced by local injection of bicuculline and muscimol into the primate motor and premotor cortex.** *J Neurophysiol* 1991, **65**:1542-1553.
 29. Tomassini V, Jbabdi S, Klein JC, Behrens TE, Pozzilli C, Matthews PM, Rushworth MF, Johansen-Berg H: **Diffusion-weighted imaging tractography-based parcellation of the human lateral premotor cortex identifies dorsal and ventral subregions with anatomical and functional specializations.** *J Neurosci* 2007, **27**:10259-10269.
- A very elegant paper where the authors use diffusion tractography to identify the border between the homologue of PMv and PMd in humans. The distinct pattern of connectivity of these two areas is also investigated and used to demonstrate that human PMv has a pattern of connections very similar to that reported in monkeys, that is, a high probability of connections with the anterior inferior parietal lobule and ventral prefrontal cortex.
30. Johansson RS, Westling G: **Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip.** *Exp Brain Res* 1988, **71**:59-71.
 31. Flanagan JR, Wing AM: **The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads.** *J Neurosci* 1997, **17**:1519-1528.
 32. Nowak DA, Hermsdörfer J, Topka H: **Deficits of predictive grip force control during object manipulation in acute stroke.** *J Neurol* 2003, **250**:850-860.
 33. Nowak DA, Hermsdörfer J, Marquardt C, Fuchs HH: **Grip and load force coupling during discrete vertical arm movements with a grasped object in cerebellar atrophy.** *Exp Brain Res* 2002, **145**:28-39.

34. Bursztyn LL, Ganesh G, Imamizu H, Kawato M, Flanagan JR: **Neural correlates of internal-model loading.** *Curr Biol* 2006, **16**:2440-2445.
35. Jenmalm P, Schmitz C, Forssberg H, Ehrsson HH: **Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts.** *J Neurosci* 2006, **26**:9015-9021.
An fMRI study showing that slow corrective increase in force during a grip-lift task, when the object is heavier than expected, activated the primary motor and somatosensory cortex. By contrast, the fast termination of excessive force, when the object was lighter than expected, specifically recruited the cerebellum. Moreover, they suggest that inferior parietal cortex plays a role in the comparison between the predicted and actual sensorimotor representation, whereas the primary sensory-motor cortex and cerebellum implement specific grip force corrections.
36. Daprati E, Sirigu A: **How we interact with objects: learning from brain lesions.** *Trends Cogn Sci* 2006, **10**:265-270.
37. De Renzi E, Motti F, Nichelli P: **Imitating gestures. A quantitative approach to ideomotor apraxia.** *Arch Neurol* 1980, **37**:6-10.
38. Koski L, Iacoboni M, Mazziotta JC: **Deconstructing apraxia: understanding disorders of intentional movement after stroke.** *Curr Opin Neurol* 2002, **15**:71-77.
39. Fadiga L, Roy AC, Fazio P, Craighero L: *Sensorimotor Foundations of Higher Cognition, Attention and Performance XXII.* Edited by Haggard P., YR, Kawato M. Oxford University Press; in press.
40. Pulvermüller F: **Brain mechanisms linking language and action.** *Nat Rev Neurosci* 2005, **6**:576-582.
A very clear review on the experimental evidence that some linguistic representations are indeed embedded within the motor system. The general hypothesis is that the complete understanding of a verb such as 'grasping' cannot rescind from the activation of the motor representation of that hand action.
41. Butterworth B: **A head for figures.** *Science* 1999, **284**:928-929.
42. Pesenti M, Thioux M, Seron X, De Volder A: **Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: a PET study.** *J Cogn Neurosci* 2000, **12**:461-479.
43. Piazza M, Mechelli A, Price CJ, Butterworth B: **Exact and approximate judgements of visual and auditory numerosity: an fMRI study.** *Brain Res* 2006, **1106**:177-188.
44. Andres M, Seron X, Olivier E: **Contribution of hand motor circuits to counting.** *J Cogn Neurosci* 2007, **19**:563-576.
This original study presents a series of experiments that aimed at identifying the cognitive processes responsible for an increased activation of hand motor circuits during counting. The results are discussed with regard to the role of finger-counting strategies in children when learning to count.
45. Glover S, Rosenbaum DA, Graham J, Dixon P: **Grasping the meaning of words.** *Exp Brain Res* 2004, **154**:103-108.
This paper provides one of the most convincing behavioural evidence for interactions between grasping and language. The results include a fine-grained analysis of the time course of the interference between grip aperture and implicit word processing.
46. Badets A, Andres M, Di Luca S, Pesenti M: **Number magnitude potentiates action judgements.** *Exp Brain Res* 2007, **180**:525-534.
This paper extends the interference between cognition and motor control to mentally simulated movements. One fascinating result is that number magnitude bias action judgements regarding the ability to grasp objects of different size, whereas perceptive judgements on the same objects are unaffected.
47. Andres M, Ostry DJ, Nicol F, Paus T: **Time course of number magnitude interference during grasping.** *Cortex*, in press.
This experiment shows that the computation of grip aperture for grasping may be influenced by abstract concepts such as numerical magnitude.
48. Rizzolatti G, Fadiga L: **Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5).** *Novartis Found Symp* 1998, **218**:81-95, discussion 95-103.
49. di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G: **Understanding motor events: a neurophysiological study.** *Exp Brain Res* 1992, **91**:176-180.
50. Rizzolatti G, Craighero L: **The mirror-neuron system.** *Annu Rev Neurosci* 2004, **27**:169-192.
51. Grafton ST, Fadiga L, Arbib MA, Rizzolatti G: **Premotor cortex activation during observation and naming of familiar tools.** *Neuroimage* 1997, **6**:231-236.
52. Grezes J, Armony JL, Rowe J, Passingham RE: **Activations related to 'mirror' and 'canonical' neurones in the human brain: an fMRI study.** *Neuroimage* 2003, **18**:928-937.
53. Craighero L, Fadiga L, Umiltà CA, Rizzolatti G: **Evidence for visuomotor priming effect.** *Neuroreport* 1996, **8**:347-349.
54. Tucker M, Ellis R: **Action priming by briefly presented objects.** *Acta Psychol (Amst)* 2004, **116**:185-203.
55. Olivier G: **Visuomotor priming of a manual reaching movement during a perceptual decision task.** *Brain Res* 2006, **1124**:81-85.
56. Fadiga L, Craighero L, Olivier E: **Human motor cortex excitability during the perception of others' action.** *Curr Opin Neurobiol* 2005, **15**:213-218.
57. Fadiga L, Fogassi L, Gallese V, Rizzolatti G: **Visuomotor neurons: ambiguity of the discharge or 'motor' perception?** *Int J Psychophysiol* 2000, **35**:165-177.
58. Binkofski F, Buccino G: **Motor functions of the Broca's region.** *Brain Lang* 2004, **89**:362-369.
59. Nishitani N, Schürmann M, Amunts K, Hari R: **Broca's region: from action to language.** *Physiology (Bethesda)* 2005, **20**:60-69.
60. Petrides M, Cadoret G, Mackey S: **Orofacial somatomotor responses in the macaque monkey homologue of Broca's area.** *Nature* 2005, **435**:1235-1238.
A paper showing that human Broca's area, the frontal region for speech production, shares cytoarchitectonic properties with monkey premotor area F5. The latter contains a vocabulary of hand actions and is the site where mirror neurons have originally been found. This homology reinforces the idea that language and action domains are strictly interconnected.
61. Nelissen K, Luppino G, Vanduffel W, Rizzolatti G, Orban GA: **Observing others: multiple action representation in the frontal lobe.** *Science* 2005, **310**:332-336.
In this very interesting paper, the authors use fMRI to investigate the functional anatomy of the mirror neuron system in the monkey. In addition, a meticulous cartilisation of ventral monkey premotor cortex is provided.